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THE MICROBIOLOGY OF FOREST SOILS A LITERATURE REVIEW

O. Hendrickson and J.B. Robinson
University of Guelph
L. Chatarpaul
Petawawa National Forestry Institute

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PETAWAWA NATIONAL FORESTRY INSTITUTE

The Petawawa National Forestry Institute was formed on April 1, 1979, as the result of an amalgamation of the former Petawawa Forest Experiment Station, which had existed for more than 60 years, with the Ottawa-based Forest Management and Forest Fire Research institutes.

In common with the rest of the Canadian Forestry Service, the Petawawa National Forestry Institute has as its objective the promotion of better management and wiser use of Canada's forest resource to the economic and social benefit of all Canadians. Because it is a national institute, particular emphasis is placed on research into problems that transcend regional boundaries or that require special expertise and expensive equipment that cannot be duplicated in CFS regional establishments. Such research is often performed in close cooperation with staff of the regional centres or provincial forest services.

Research at the institute is in two main areas:

FIRE RESEARCH AND REMOTE SENSING. Every year in Canada large areas of productive forest are destroyed by fire. Research concentrates on studies of forest fire behaviour, the development of new methods of fire control, the evaluation of fire-fighting equipment and retardants, and the development of computerized fire management systems that are rapidly finding applications with fire-fighting agencies across the country. The environmental and economic impact of forest fires and the use of fire as a silvicultural tool for intensive forest management are also studied.

In remote sensing, investigations are made into the application of modern satellite and airborne remote sensing systems to forestry problems. In this respect, the ARIES digital image analysis system is proving invaluable.

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In support of its research programs, the institute has at its disposal a 98-km^2 area of forest in the northern part of the Petawawa military reserve. Records of experiments and sample plots have been maintained since the 1920s. The forest also serves as a field laboratory for students from local schools, and a visitor centre is operated during the summer months.

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O. Hendrickson and J.B. Robinson
Dept. of Environmental Biology
University of Guelph, Guelph, Ontario

L. Chatarpaul
Petawawa National Forestry Institute
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FOREWORD

ENFOR is the acronym for the Canadian Government's ENergy from the FORest (ENergie de la FORêt) program of research and development aimed at securing the knowledge and technical competence to facilitate, in the medium to long-term, a greatly increased contribution from forest biomass to our nation's primary energy production. This program is part of a much larger federal government initiative to promote the development and use of renewable energy as a means of reducing dependence on petroleum and other non-renewable energy sources.

The Canadian Forestry Service (CFS) administers the ENFOR Biomass Production program component which deals with such forest-oriented subjects as inventory, harvesting technology, silviculture and environmental impacts. (The other component, Biomass Conversion, deals with the technology of converting biomass to energy or fuels, and is administered by the Renewable Energy Branch of the Department of Energy, Mines and Resources). Most Biomass Production projects, although developed by CFS scientists in the light of ENFOR program objectives, are carried out under contract by forestry consultants and research specialists. Contractors are selected in accordance with science procurement tendering procedures of the Department of Supply and Services. For further information on the ENFOR Biomass Production program, contact

ENFOR Secretariat
Canadian Forestry Service
Department of the Environment
Ottawa, Ontario
K1A 1G5

or a CFS research laboratory.

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THE MICROBIOLOGY OF FOREST SOILS
A LITERATURE REVIEW

O. Hendrickson[1], J.B. Robinson[1] and L. Chatarpaul[2]

ABSTRACT

This report discusses the activities of two major groups of forest soil microorganisms, the bacteria and the fungi. Special attention is paid to their participation in the decay of major forest litter substrates, including leaves, branches and roots. The influence of bacteria and fungi in symbiotic associations with woody plant roots upon the cycles of carbon and nitrogen is described. The impacts of certain forest management alternatives are assessed in terms of the creation or elimination of suitable environments for the activity of soil microorganisms.

RÉSUMÉ

Le présent rapport traite de deux groupes importants de micro-organismes que l'on trouve dans les sols forestiers, soit les bactéries et les champignons. On porte une attention particulière à la façon dont ces organismes participent à la décomposition des principaux débris de la litière, notamment les feuilles, les branches et les racines. On y décrit l'influence des bactéries et des champignons en association symbiotique avec des racines de plantes ligneuses sur le cycle du carbone et celui de l'azote. Les répercussions de certaines méthodes de gestion forestière sont évaluées en fonction de la création ou de l'élimination de milieux convenant aux activités de ces micro-organismes.

1. INTRODUCTION

Forest soils may develop in a variety of ways depending on such factors as geographic location, climatic conditions, topography, parent material and plant species. In the boreal forest which has developed in the precambrian shield of Northern Ontario, the soils are generally well podsolized acid mors, similar in many characteristics to certain forest soils of northern Europe. These soils are characterized by deep organic layers in which L, F and H horizons can usually be distinguished, and with well-developed A_2 horizons.

Studies on the microbiology of Ontario's forest soils have been infrequent and have not succeeded in developing a comprehensive understanding of the microflora of these soils and of the microbial processes occurring in them. In Ontario as elsewhere, microbiologists have found forest soils to be difficult subjects for study. The spongey organic layers do not lend themselves to the techniques which have been developed for the study of agricultural soils. In fact, generalizations based on experience with the agricultural environment may have limited applicability in forest soils. While mineralization activity is distributed throughout the plow layer in agricultural soils, it tends to become concentrated in forest soil organic horizons. The acid reaction of many forest soils is thought to

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[1] Ole Hendrickson and John B. Robinson are Research Fellow and Professor respectively in the Department of Environmental Biology, University of Guelph.

[2] Lake Chatarpaul is a research scientist at the Petawawa National Forestry Institute.

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favor fungal activity, but alkaline microsites may support a flourishing bacterial flora. Certain unique acid tolerant bacteria may also be present. Interactions between microorganisms and roots play an increasingly important role in forest soils, although these rhizosphere associations are similar to those found in the agricultural environment.

In preparation for an investigation of the impact of harvesting procedures on microbiological processes in an Ontario forest soil, we have made a survey of the pertinent literature. This review deals with selected topics from that survey. We have tried to focus discussion on topics which have significance to acid mors or which are likely to be important in our study of harvest impacts.

Most forest scientists recognize the importance of microbial decay in regenerating nutrients essential for tree growth. In agriculture, essential elements can be supplemented by fertilization. The manager can calculate appropriate timing and amount for a nutrient supplied to a given crop. Due to economic constraints, this option is often not available to the forest manager. He must depend upon microbial nutrient cycling to produce a healthy stand of trees.

Management options are nonetheless open to the forester. The considerable potential for enhancing nitrogen supply, by selection of appropriate nitrogen-fixing bacteria and host tree species, has led to a recent explosion of research activity. Current interest in mycorrhizal fungi is also great. The roots of woody plants are coming to be viewed as multi-species symbiotic associations. Each partner in the symbiosis is a potential candidate for management via selection, genetic improvement, and large-scale culturing and inoculation techniques.

Various harvesting and site preparation techniques also have a major impact on microbial processes in forest soils. Reduced quantities of slash remaining after whole-tree cutting will limit the growth of decay fungi and the eventual return of mineral nutrients to the soil. Fire reduces organic substrates, but also acts as a mineralizing agent and may thereby increase the activity of certain groups of microorganisms. Herbicides used to control hardwoods may reduce populations of certain groups of fungi; conversely, deliberate interplanting of hardwood and conifer species might be used to increase microbial diversity and enhance litter decay. Any thinning or selective cutting operations which produce altered temperature and moisture conditions at the soil surface will concurrently alter microbial populations and processes.

The advantages to the forest scientist of acquiring a working knowledge of soil microbiology are evident. It is our aim in this review to facilitate this acquisition. The literature search was terminated in April, 1982.

2. THE FOREST SOIL MICROFLORA

Microbial processes in forest soils are dominated by two rather distinct groups of organisms - the bacteria (including actinomycetes) and the fungi. Bacteria are primitive in that they do not divide by mitosis, lack cellular inclusions such as mitochondria, chloroplasts and nuclei, and do not show extensive differentiation of tissues or specialized cells. They are classified as prokaryotes, meaning "before nuclei". In an evolutionary sense bacteria are the oldest living creatures, having probably appeared more than 3 billion years ago. They evolved under an oxygen-free atmosphere, and many still tolerate or absolutely require anaerobic conditions. Their small size (0.5 to 40 microns) and simple structure may be contrasted with a diverse array of metabolic pathways. One group of bacteria, termed "chemoautotrophs", can obtain their carbon and energy requirements strictly from inorganic precursors. These include the important group of nitrifying bacteria (which oxidize ammonium to nitrite and nitrate) as well as the sulfur and methane oxidizers. The process of nitrogen fixation, which is the ultimate source of all organic nitrogen in living biomass, occurs only in prokaryotes, whether free-living or in symbiotic association with higher organisms.

Fungi appeared much later in the earth's evolutionary history, around 450 million years ago, concurrent with or slightly following the development of higher plants in terrestrial environments. Fungi are eukaryotes, possessing mitochondria and nuclei, and undergoing mitotic cell division. Some develop complex and highly differentiated tissues, such as the reproductive structures of basidiomycetes (i.e. sporocarps or mushrooms). Most are limited to aerobic conditions, and all require fixed organic carbon for growth and energy.

Microbiologists by convention study both bacteria and fungi, though most specialize in one particular group. A knowledge of both groups is essential for an understanding of forest nutrient dynamics. Interactions between bacteria and fungi are very common: the symbiosis of fungi and cyanobacteria found in lichens, the loose-knit relationship between mycorrhizal fungi and various gram-negative bacteria in the rhizosphere, and the antagonism and lysis of fungal hyphae by actinomycetes are but a few examples.

Other groups of organisms are often studied by microbiologists. Unicellular amoebae, ciliates, and flagellates can be very numerous in forest soils. Although they may graze actively on fungi and bacteria and control their numbers, they will not be discussed in any detail in this review. The soil fauna including nematodes, mites, collembola, and earthworms - is also quite important in influencing microbial populations, especially during the processing of leaf litter. A brief discussion of this interaction between soil animals and microorganisms can be found in the section on leaf litter decay.

2.1. Bacteria and actinomycetes

It is difficult to generalize about the bacterial flora of forest soils. Jensen (1962) argued that high taxonomic variability was characteristic and that the "microbiological equilibrium is far less stable" than in agricultural soils. He found that Gram-negative, non-pigmented rods such as Pseudomonas and Achromobacter are dominant in European forests, along with the streptomycetes. In mull soils, usually found under deciduous trees, pigmented rods (Flavobacterium, Chromobacterium) and Gram-variable, pleomorphic rods (Corynebacterium, Arthrobacter, Nocardia) are also found. Spore-forming bacteria such as Bacillus cereus are relatively more common in mor (coniferous) soils. A clear difference may be seen from agricultural soils, were Arthrobacter is often the dominant organism. The forest bacterial flora was said by Jensen to resemble that of the root surfaces of crop plants (the rhizosphere) described by Lochhead and Thexton (1947). His observations in Danish soils are largely corroborated by studies of an English pine forest (Freshfield), which recently formed on sand dunes (Goodfellow et al. 1967, Goodfellow 1968). In this pine forest, spore-forming bacteria (Bacillus spp.) are relatively more common than the non-pigmented rods, but both groups are clearly dominant in the A_2 horizon. The organic horizon of the Freshfield soil resembles the peat soil described by Holding et al (1965) where Bacillus spp. makes up 67% of the bacterial isolates.

It is interesting that later work in Denmark and England has shown greater similarity between agricultural and forest soils. Arthrobacter is found to be relatively more abundant in forests if care is taken to pick out leaf litter and roots from the 'actual' soil. Goodfellow and Dawson (1978) used very small (5g) soil samples to show that Gram-negative species are mostly present in recently fallen pine needles, and are replaced by Arthrobacter and Streptomyces in the litter layer. Holm and Jensen (1972) used sterile gloves to pick out surface litter material and removed all roots by sieving. They found a mixture of Arthrobacter spp. with Gram-negative pigmented and non-pigmented rods in the organic horizon of a beech wood. These findings emphasize the difficulty of making quantitative counts of bacteria in forest soils. Populations may be strongly related to specific substrates. Choice of sampling methods and sample preparation in the lab will greatly influence results.

An alternative to studies of the microflora of "bulk" samples is an "autecological" approach, a study of the distribution and activity of given species within the soil environment. The preparation and use of fluorescent antisera specific for *Bacillus subtilis* and *B. circulans* was described by Hill and Gray (1967). They were able to observe these species as they occurred naturally in microsites of an English pine forest soil (Freshfield). On mineral particles, *B. subtilis* was found as small ($< 2\mu$), straight rods, in colonies of 1 to 14 cells. More commonly, it was observed on organic particles as long (4-11μ) curved rods in colonies of 1-40 cells. Cells growing in liquid media were quite unlike those in soil. This was also the case for *B. circulans*, which formed clusters of cocci or short rods on soil organic matter, unlike the characteristic long cells seen in culture. Further studies (Gray 1973, Siala et al. 1974) indicate that spore germination and growth of *Bacillus* spp. occurs largely in association with living and dead fungal hyphae. No growth is found in sterile soil. In the acid A_1 horizon of the Freshfield soil, 70% of the population of *Bacillus* was present as active cells, largely on various plant remains. Most of the population (70-90%) in the alkaline C horizon occurred as spores, which were affixed to iron-coated sand grains. The authors suggested that an earlier belief that *B. subtilis* is usually present as spores in acid soil requires modification, and that its activity suggests a lower pH tolerance in soil than in culture. A key point in understanding the ecology of *Bacillus* is its association with decay of fungal hyphae.

In a subsequent investigation of the Freshfield soil, Lowe and Gray (1972, 1973a) identified 209 isolates of non-sporing coccoid bacteria which could be assigned to seven "principal species clusters"--2 *Micrococcus*, 1 *Staphylococcus*, and 4 *Arthrobacter*. None of these species grew in the acid A_1 horizon although four of them had been isolated from it. Growth occurred only if the pH was increased to 5.5 or above by adding $CaCO_3$. Addition of glucose or amino acids did not induce growth. Artificial "alkaline microenvironments" could be created by amending soil with chitin, ground fungal mycelium, or yeast cells; and inoculating with a viable fungal culture (*Trichoderma*, *Mortierella*). *Arthrobacter* could then become active. If spores of *T. viride* were added simultaneously with *Arthrobacter* cells, no growth of Arthrobacter occurred. If the bacteria were added 18 hours after the fungus, numbers declined initially and then increased. This suggested that as the fungus mineralized organic materials and released ammonia, increased pH gradually created a suitable habitat for *Arthrobacter*. Hissett and Gray (1976) have reviewed the role of microsites in forest soil microbial ecology.

A different mode of survival was exhibited by actinomycetes in the Freshfield soil (Williams and Mayfield 1971, Mayfield et al. 1972, Ruddick and Williams 1972). They were found as spores in the acid A_1 horizon. Germination could be induced by adding nutrients. Acid tolerant actinomycetes can germinate in sterile soil, while "neutrophilic" species grow only where fungal activities create microsites of high pH. Electron microscopy shows actinomycete spore chains and mycelia on a variety of organic substrates: roots, bark, leaf fragments, twigs, pine needles, and decaying fungal hyphae. Spores are transported readily through soil, and are therefore important in colonization of fresh substrates. Hydrophobic spores of *Streptomyces griseus* may be isolated from a variety of soil arthropods, and are seen in electron micrographs to be carried on the body and legs. An elegant demonstration of spore transport can be made by allowing a mite to walk across a petri plate, leaving behind spore "footprints" which develop into actinomycete colonies. Soil animals greatly facilitate spore dispersal in the upper layers of soil, while spore movement in lower layers is governed by pore geometry and the electrostatic properties of soil colloids.

Actinomycetes were once thought to be rare in forest soils, due to an intolerance of low pH. Jensen (1928) described and named an acid-tolerant species-group of actinomycetes found in peat and organic forest soil. These organisms grow on acid (pH 4.0) agar used for counting fungi, but not on the pH 6.5 agar used for bacteria and actinomycetes. Corke and Chase (1964) used media buffered at a range of pH values from 3.0 to 7.0 to demonstrate large actinomycete populations, in the order of 6×10^6 g^{-1}, in the organic horizon of an acid podzol under pines. Williams et al. (1971) reported numbers of 2×10^6 g^{-1} in the combined F_2/H horizon of the Freshfield soil discussed earlier. The "acidophilic" species, with pH optima of 4.5, were abundant in the organic soil but absent from the alkaline C horizon. The "neutrophiles" were present in small numbers in the surface layers but increased to 500,000 g^{-1} in the upper C horizon. Their pH optimum was 7.0. Extremely high actinomycete populations have also been reported in wet, acid soils of the Pacific Northwest region, comprising 65% of the "total bacteria" in mixed alder-conifer stands, and 45% under conifers alone (Lu et al. 1968). Numbers may reach 75×10^6 g^{-1} in these soils (Wright and Bollen 1961).

Despite the great numbers of actinomycetes present in certain forest soils, little is known of their metabolism. Considine and Casida (1964) found colonies of actinomycetes growing on a medium selective for aerobic nitrogen fixing bacteria. They inhibited *Azotobacter* colonies. A requirement for cobalt, molybdenum, and citrate suggested that these could be free-living nitrogen fixers. Symbiotic nitrogen fixing actinomycetes of the genus *Frankia* inhabit root nodules of plants like alder. Actinomycetes will attack humic acids, chitin, and other relatively resistant organic compounds (Lacey 1973), and lignocellulose decomposition by *Streptomyces* was reported recently (Crawford 1978). An occasional plea is made for more study of the substrate relationships and activities of this group (e.g., Wright and Bollen 1961).

Other groups of bacteria are either less common in the forest environment or have received inadequate attention. Significant increases in populations of nitrifying bacteria have been noted after clear-cutting (Smith et al 1968), associated with increased nitrate levels. Some work has been reported on nitrogen-fixing species. It is thought that most asymbiotic nitrogen-fixing activity is due to facultative anaerobes such as *Bacillus* and *Clostridium* spp., while the aerobic nitrogen fixer *Azotobacter* is rare in forest soil (Chang and Knowles 1965, Jurgensen and Davey 1971).

Anaerobic bacteria (Skinner 1967) are seldom studied from the viewpoint of their activities in forest soil; indeed, any comment on the extent of anaerobic metabolism in forests would be largely speculative. A series of papers on catalase-negative soil bacteria (Casida 1965; Gledhill and Casida 1969a, b, and c) proposed that these "microaerophiles", possessing characteristics transitional between aerobic and anaerobic actinomycetes, might be the most abundant group of soil microorganisms. The presence of poly-amino butyric acid in the cell wall was a distinguishing trait. It would be interesting to know if these organisms could be isolated from forest soils as well as the agricultural soils studied by these authors.

Bacteria in the root environment, or rhizosphere, have received considerable attention. Discussion of this topic will be deferred to a later section.

2.2. The fungi

Fungi appearing on petri plates of agar are largely those species of phycomycetes and Fungi Imperfecti which produce abundant spores. This was shown convincingly by Warcup (1955), who removed colonies forming on plates at 18 hours after inoculation. By subculturing and careful microscopic examination, he concluded that the majority originated from spores, and that many hyphae were not counted. These abundantly sporing organisms largely fall into the classification of "sugar fungi", a designation proposed by Burges (1939). Their growth is similar to actinomycetes: they germinate when substrates are available, grow and reproduce quickly, and assume resting forms when substrates are depleted. Phycomycete mycelia, in particular, do not persist, but quickly disintegrate as spores are formed (Burges 1963a). Mycelial contents appear to be translocated to the growing tips, leaving behind empty cell walls (Harley 1971). By contrast, the hyphae of "higher fungi", especially the basidiomycetes, are quite persistent in soil. Vacuoles may form, but cytoplasmic continuity tends to be retained. The hyphae do not commonly fragment and produce "chlamydospores". Burges (1963a) noted that basidiomycetes respond quickly to nutrient additions, much like a washed cell suspension. However, they are not adapted for rapid germination and growth on solid agar media, and are almost never isolated from dilution plates. Parkinson (1973) commented on the "elusiveness" of basidiomycetes:

> "It is particularly unfortunate in studies of forest litter fungi where one expects to find cellulose decomposing species, lignin decomposing species and mycorrhizal species and one can frequently see the macroscopic basidiomycete fruiting structures on the forest floor and where microscopic examination of litter frequently reveals the presence of clamp-bearing hyphae."

Harley (1971) pointed out that rapid assimilation and retention of essential nutrients in fungal mycelia may result in the growth of other organisms being limited by the rate at which the fungi decompose. One the other hand, their richness can make them important food sources for soil animals.

Various methods have been devised to distinguish between actively growing mycelium and spores. Chesters (1940, 1948) described the use of an "immersion tube", a glass rod containing fine, agar-filled capillaries, into which mycelia grew and could then be isolated. He assumed that the capillaries would be most readily colonized by mycelia already present in the soil, but could not exclude the possibility that spores might germinate and grow into them. Warcup (1960) described a method for dissecting hyphal tips from soil and plating them individually. This has not been widely used due to its difficulty. Probably the most important advance was the introduction of techniques where soil, roots, leaves, etc. are cleaned of spores by repeated washings, and the washed particles are then plated directly. Harley and Waid (1955) showed that surface fungal populations of washed roots differed greatly from the fungi found in the wash water. Parkinson and Williams (1961) obtained similar results for washed soil particles. Soil washing is now frequently used in taxonomic surveys of fungi, as it reveals a more diverse microflora. Often, a series of screens are mounted within a box, with the smallest mesh size near the bottom. Sterile water is repeatedly flushed through the soil sample, and particles collecting on the finest screen are plated (Hering 1966a, Bissett and Widden 1972). Even using this technique, basidiomycete hyphae are rarely isolated.

The work of Bisby et al. (1933, 1935) illustrates the approach of the early fungal taxonomists. Their first study dealt mainly with cultivated fields, from which species of Penicillium, Fusarium, Trichoderma, Rhizopus, Cladosporium, Gliocladium, Aspergillus, Cephalosporum, Alternaria, etc. were the most common isolates, in order of abundance. Subsequently they sampled virgin soil profiles, especially in forests, and found large numbers of phycomycetes, especially Mortierella, Mucor, and Absidia. Even so, Penicillium still accounted for about 50% of their forest soil isolates, and Trichoderma was also common. Aspergillus and Fusarium apppeared to be rare, characterizing agricultural rather than forest environments. The fungal microflora of peat contained a unique collection of *Penicillium* spp. and abundant *Mortierella* spp., although numbers decreased rapidly with depth. Anaerobic fungi capable of growth in a 100% CO_2 atmosphere included species of *Trichoderma*, *Cylindrocarpon*, and some of the phycomycetes, with a noticeable depletion of *Penicillium* spp. As much as 50% of the population in the B and C horizons of certain profiles could be cultured anaerobically. Another group of fungi were characterized by growth at 7°C; these also increased with depth.

A number of studies have examined the question of whether microfungal populations can be used to characterize different forest stands. Using sophisticated statistical methods, mature forest communities have been compared with secondary forests developing after fire or clear cuttings. To some extent, microfungal changes reflect the speed and direction of plant community succession. This approach was introduced by Tresner et al. (1954), who listed characteristic "climax" fungal species (*Penicillium nigricans*, *Spicaria violacea*), "pioneer" species (*Mucor ramannianus*, *P. janthinellum*), and "indicator" species for certain soil types in Wisconsin. They found a distinct community of slow-growing forms at lower depths in the soil profile which differed from the faster growing forms in the upper layers, but excluded these from taxonomic consideration due to difficulties in culturing. Although no discrete microfungal communities were found in the upper profile, they felt there could be a continuum of similarity within microfungal distributions analogous to that of tree species.

Their arguments, although persuasive, must be tempered by findings that microfungal populations reflect environmental conditions (moist vs dry environments, soil texture) and substrate availability (woody residue, leaf litter types) to a point that may obscure community relationships. Christensen and Whittingham (1965) found characteristic groups of fungi in open bogs, spruce-tamarack swamps, and cedar-fir swamps in Wisconsin, but many of the species were common wood, wood pulp, and litter forms. A comparison with the microflora of drier conifer-hardwood forests (Christensen 1969) revealed that many species were widely distributed in all soils. Only *Mortierella vinacea* and *M. nana* were characteristic of conifer and conifer-hardwood soils. Fungal populations were better differentiated on the basis of litter calcium (low under pines) than by a moisture gradient. Sand-bar willow stands along the Wisconsin River contained many fungi characteristic of sand dunes and desert areas, with thick-walled hyphae or various reproductive structures as adaptations to periodic dessication (Gochenaur and Backus 1967). Only *Mucor hiemalis* was common among the phycomycetes. This group, which often dominates species lists from forests, comprised only 10% of the identified sand-bar species.

A comparison of fungi in forest and cultivated soils of Georgia (Miller et al. 1957) indicated that *Penicillium* spp. and the various Mucorales (*Mortierella*, *Absidia*, *Zygorhynchus*) were common in forests, *Fusarium* and *Aspergillus* in fields. Thus, the overall trend was identical to that found in Manitoba by Bisby et al. (1933, 1935). A pinewood soil in Britain (Ellis 1940) showed a characteristic differentiation between high temperature surface fungi (e.g., *Trichoderma*) and low temperature fungi at depth (*Mucor*, *Penicillium*, and *Cylindrocarpon* spp.) also comparable to findings in Manitoba. Thornton (1956) felt that the distribution of species within the Mucorales might indicate varying degrees of acidity within forest soils, with *Mortierella humilis*, *M. nana* and *M. stylospora* found in less acid brown forest soils and *M. ramannianus* and *M. gracilis* in acid podzols. Dominant microfungi of a boreal forest in Saskatchewan (Morrall and Vanterpool 1968) were reported as *Mortierella* spp., *Penicillium* spp., and *Oidiodendron* spp., with *Aspergillus* and *Fusarium* absent. A similarity with the Wisconsin forest studies was noted. Reddy and Knowles

(1965) used the soil washing technique to study a boreal forest in Quebec, and found that *Penicillium* spp., *Aureobasidium*, and yeasts dominated the washings, while the Mucorales were greatly increased on the washed soil particles. Fertilization with urea, which increased soil pH, eliminated many of the Mucorales. These authors reported difficulties in applying washing techniques to organic particles in the F layer, finding relatively high numbers of organisms in the water after repeated washings. Many studies, such as that of Widden (1979) comparing fungi in deciduous and forest soils in southern Quebec, are limited to the mineral soil. This is due in part to difficulties in finding a technique suitable for quantitative studies of the overlying organic layers.

Numerous studies have described changes in fungal populations with depth. Williams (1963) and Williams and Parkinson (1964) found relatively few species in the lower soil horizons, where the environment is considerably more stable than at the surface. Populations in these lower horizons showed no seasonal fluctuations. *Phialophora* sp. was found to follow the distribution of roots in mineral soil. Other species increasing with depth, such as *Trichoderma album* and *Paecilomyces* sp., were found indiscriminately on humus particles and root fragments. Subsoil fungi tend to comprise a unique and distinctive group. Soderstrom and Baath (1978) remarked that "two soil horizons only a few centimeters apart show greater differences than identical horizons hundreds of kilometres apart." Different groups of *Mortierella* spp. were found within the separate horizons of a podzol, and *Oidiodendron* and *Tolypocladium* increased with depth. *Tolypocladium* was shown to have a powerful antagonistic action on a wide variety of organisms, far greater than better-known antibiotic producers such as *Trichoderma viride*. It was suggested that antibiotic production is especially important for slow growing species in relatively harsh environments (Lundgren, Baath and Soderstrom 1978). Jensen (1963a) also found that certain *Mortierella* spp., particularly *M. nana*, characterized the subsoil of a Danish beech forest. A survey of several coniferous forest sites in Canada (Widden and Parkinson 1973) indicated that the subsoil microflora may be site-specific. *Paecilomyces variabilis* and *Torulomyces lagena* were dominant in Ontario, while *Verticillium chrysosporium* and *Oidiodendron* were found in the Alberta mountains.

Burges (1963b) described the appearance of fungal hyphae in the various mineral soil horizons. In the A_1, hyphae tend to be associated with masses of organic matter, and various types intermingle. Unbranched hyphae extend for relatively long distances through mineral soil when traversing between two organic particles. Hyphae in the B horizon are associated with sand grains, but seem to be old and "partially mummified by encrusting humic acid". He suggested that these hyphae are relatively immune to attack from soil animals and bacteria and persist long after death. Although hyphae are very scarce in the C horizon, most tend to occur in aggregates.

Organisms found deep within soils are likely to be successful competitors for scarce food resources, and in the colder regions must grow efficiently at low temperatures. In contrast, surface soils have more varied substrate inputs and fluctuating environmental conditions, which create opportunities for fast growing or relatively specialized organisms. It has been shown that each of the surface organic horizons (L, F, H) within a mor profile possesses its own characteristic microflora. This represents a succession of organisms colonizing litter materials in increasing stages of decay.

Although any of three major groups of fungi-yeasts, ascomycetes and basidiomycetes-may be dominant in numbers and/or biomass in certain situations, they have received less attention than the phycomycetes and Fungi Imperfecti. Jensen (1963b) reported yeast populations of up to 100,000 g^{-1} in mull and 500,000 g^{-1} in mor soils. He indicated that many yeasts are intolerant of the low pH in conventional fungal media, which might account for the low numbers reported in many studies. His typical soil yeasts (Candida, Torulopsis) were nonfermentative, fast-growing carbohydrate decomposers which tolerated mildly acid to alkaline conditions. They showed nutritional and biochemical similarities to "sugar fungi." Reddy and Knowles (1965) noted increased yeast populations in conifer forests after urea fertilization, which created more alkaline conditions. di Menna (1960) indicated that yeasts in New Zealand were less abundant in forests than in pastures, and her maximum counts (30,000 g^{-1}) were much lower than Jensen's. Soil amoebae readily consume yeasts, (Heal 1963) so their numbers may fluctuate quickly.

As noted earlier, basidiomycetes do not grow readily on agar, and are therefore generally not included in taxonomic surveys of fungi. Russell (1956) was able to enhance the selectivity of malt agar medium by incorporating o-phenyl phenol, which is relatively toxic to the microfungi. The hyphal isolation technique has been used to show that basidiomycetes are common in cultivated soils, where sporocarps are rarely seen (Warcup 1959; Warcup and Talbot 1962). Basidiomycete hyphae can be identified by their characteristic "clamp connections", but fructification must be induced to make positive identification to species. This is a difficult and laborious task. Recent work indicated that isoenzyme patterns of laccase, esterase and amylase could be used to distinguish mycelia of four species of wood rotting basidiomycetes (Schuster and Jung 1981).

A number of studies have shown that the biomass of basidiomycete sporocarps alone can be considerable in some forests (Hora 1959, Hering 1966b, Richardson 1970). Harley (1971) calculated that, if all basidiomycete fruiting bodies were mycorrhizal, and their carbon requirements were totally supplied by the host trees, their production could require as much as 10% of the net photo-synthesis of the vascular flora. The quantification of the mycelial biomass of basidiomycetes is an extremely difficult problem, although the fluorescent antibody technique being developed by Frankland et al. (1981) seems promising.

2.3. Microbial interactions

Antibiotic production by microorganisms is often used to explain observed antagonisms in soil, yet this can generally not be proven due to the small amounts of compounds involved. Weindling (1932, 1934, 1937) observed that Trichoderma viride, growing in the vicinity of the pathogenic root fungus Rhizoctonia solani, was able to cause the hyphae of the latter fungus to fill with dark, yellow material, often leading to autolysis or breakage at a septum. He suggested that a "lethal principle" was involved. This substance was apparently broken down quickly in culture, especially at high pH levels. Its action could be nullified by absorption on charcoal. In 1937, Weindling successfully isolated the lethal principle, which he named gliotoxin. Subsequent work showed that T. viride produced a substance even more toxic to other fungi, which was called viridin (Brian and McCowan 1945). Many people assumed that Trichoderma viride would subsequently find wide application as a biological control agent, but this hope has so far gone unfulfilled. Jeffreys et al. (1953) isolated 65 species of microfungi from an acid heath soil, and demonstrated that fully half of them had some antibiotic activity. Only phycomycetes, the fast-growing "sugar fungi", showed no production of fungistatic compounds. Some evidence was found that phycomycetes were nonetheless relatively resistant to antibiotics produced by other species. Park (1960) stressed the importance of antibiotic tolerance, arguing that this strengthened his hypothesis that antibiosis can generally account for observed antagonisms in soil.

One such antagonism, studied by Dobbs and Hinson (1953), was the failure of fungal spores to germinate when added to soil. Spores which germinated readily in water showed no growth even in moist soil. Certain treatments did permit spore germination in soil: autoclaving, prolonged air drying, glucose additions, mixing in very finely divided charcoal. A "widespread fungistatic factor" was postulated to exist in soil, perhaps an organic compound. Fungistasis was suggested to be of actual benefit to the inhibited organism in some cases, in that it prevented development where nutrients were inadequate for support of vegetative growth. Subsequent investigations (Dobbs et al. 1960) indicated that the general dormancy of spores in soil was not as universal a phenomenon as was originally proposed, since the strength of inhibition appeared to vary seasonally, being considerably reduced in winter. Some forest humus samples did not exhibit fungistasis, and could even counteract it when added to other soils.

Lingappa and Lockwood (1961) continued these studies of fungistasis. They ruled out the possibility that volatile substances were involved, showed that sugars and amino acids gave varying counteractive effects, and observed that many spores added to soil disappeared altogether, apparently consumed by other organisms. They suggested that spores served as "nutrient microsubstrates" in soil, and that rapid growth of soil microbes in their vicinity led to production of sufficient fungistatic substance to prevent germination. By inoculating sterilized soil with various microorganisms, they found that all bacteria, fungi and actinomycetes tested could inhibit fungal spore germination (Lockwood and Lingappa 1963). When spores were added to non-sterile soil, O_2 uptake increased measurably. Similar results could be obtained by adding killed spores or cell-free spore washings. Thus they suggested that consumption of spore exudates or the spores themselves was responsible for the increased respiration (Lingappa and Lockwood 1964). Streptomycete isolates were found to exhibit two modes of action against fungal spores. Antibiotic-producing strains produced spore inhibition zones whose size was independent of the nutrient concentration in the agar medium. Strains lacking antibiotics produced inhibition zones which became progressively smaller as the nutrient content of agar was increased. These variable-sized inhibition zones could be simulated by leaching nutrients from the agar at different rates with running water (Hsu and Lockwood 1969). Finally, a rather elaborate system was devised to show that fungistasis could be wholly explained by microbial uptake of spore exudates (Sneh and Lockwood 1976). ^{14}C-labelled spores of Lochliobolus victoriae were produced by growing mycelia in ^{14}C-glucose media. These were spread on sterile filter paper on an apparatus in which they could be leached at varying rates. The exudates produced were collected, concentrated, and measured in a scintillation counter. Spore exudation on soil was measured indirectly by measuring labelled $^{14}CO_2$ evolved by microorganisms consuming exudates. Slow leaching rates allowed spores to germinate despite considerable exudate removal, but increasing leaching rates prevented germination. Even the highest flow rates attainable with the leaching device did not remove as much exudate as was evolved as $^{14}CO_2$ from soil, however. It was concluded that soil acted as a highly effective "nutrient sink" for spore exudates, well in excess of that required for fungistasis. Where nutrient competition was less severe, spores could retain or reabsorb their own exudates, allowing the germ tube to be synthesized.

Antibiosis and competition are both likely causes of antagonisms. Park (1955; 1957) compared the behavior of two groups of fungi in the presence of cultures of Bacillus spp. Indigenous soil fungi (Mucor, Fusarium, Penicillium, etc.) successfully colonized soil with added plant materials by germinating, producing small amounts of viable mycelium, sporulating, and repeating this cycle. Their spread was often slow, and short hyphal segments were broken up by areas which had been consumed by bacteria. "Alien" fungi could survive only by producing thick walled resting spores. If they germinated, they could not survive in competition with Bacillus, which often caused their hyphae to lyse. The general lytic ability possessed by Bacillus spp. is reflected in enzymes such as chitinase and laminarinase, which act on fungal cell wall components (Mitchell and Alexander 1963).

Fungi act as substrates for bacteria and actinomycetes in soil, but according to Lockwood (1968), the nature of the interaction depends on nutrient availability. A fungus which has better growth due to favourable nutrient levels is better able to withstand attacks of bacteria and streptomycetes. Lockwood (1968) argued that lysis is never a direct attack on the living fungus, but is mediated by nutrient competition. The fungus starves, and autolysis occurs rather than external lysis. Dickinson et al. (1981) disagreed with this interpretation of nutrient competition. They stressed that when an actinomycete "antagonizes" a fungal hypha, it is not competing for nutrients, but obtaining them directly from the fungus. They observed that germination of streptomycete condia was generally stimulated in the presence of fungal hyphae. Hyphal lysis by the actinomycete was not necessarily advantageous, as it might obtain more nutrients by avoiding such "hyperparasitic" activity. It thereby could extend its own filaments at the expense of those of the fungus.

Competition also occurs among different bacterial species. Chan et al. (1963) grew mixed bacterial cultures consisting of five species (*Agrobacterium radiobacter*, *Arthrobacter citreus*, *Azotobacter chroococcum*, *Bacillus cereus*, *Pseudomonas* sp.) on both soil extract and root extracts. *Arthrobacter* was the dominant organism in soil extract, while *Pseudomonas* predominated in root extract. *Bacillus* and *Azotobacter* fared poorly in both media. Rather surprisingly, closely related organisms appear to compete less than more distantly related species. Several well-differentiated species of coccoid bacteria showed no tendency to displace one another when grown together on petri plates. (Lowe and Gray 1973b). By contrast, *Pseudomonas* and *Arthrobacter* showed marked competitive interactions in culture (Sieburth 1967). Two inhibitory compounds were produced by *Pseudomonas*: a gummy substance which caused *Arthrobacter* cells to clump together, and an antibiotic substance with direct inhibitory effect. When *Pseudomonas* was maintained in pure culture for any length of time it lost the ability to produce these compounds.

Various hypotheses have been put forward to explain why gram-negative species such as *Pseudomonas* predominate in the rhizosphere, while *Arthrobacter* - like species are more common in mineral soil. One obvious explanation is that rhizosphere species are preferentially stimulated by root exudates. Chan and Katznelson (1961) noted a general tendency for Gram-negative pseudomonads to produce acid, fluorescent pigments directly suppressing the growth of non-rhizosphere species. The inability of *Pseudomonas* to compete successfully with *Arthrobacter* in mineral soil might be due simply to different responses to drying. By making plate counts of these organisms at regular intervals during drying, Robinson et al. (1965) observed that *P. fluorescens* showed a rapid decline, disappearing in dried soil after one month. It appeared to be eliminated faster in mixed culture, unlike *Arthrobacter*, which was relatively unaffected by drying regardless of the presence of other organisms. A similar experiment by Chen and Alexander (1973) showed that *Arthrobacter* persisted for 90 days in desicated soil. *Bacillus* spp. and certain actinomycetes also survived by producing spores.

Not all microbial interactions in forest soil are competitive or antagonistic in nature. Rhizosphere associations of mycorrhizal basidiomycetes and Gram-negative pseudomonads appear to be mutually beneficial, in that higher bacterial populations appear to be associated with mycorrhizal as opposed to uninfected roots (Katznelson et al. 1962). Bacterial nitrogen fixation is thought to represent a significant input of nitrogen in certain stages of woody litter decay, aiding the activity of lignin-degrading fungi. Numerous other examples of cooperative interactions occur during microbial successions on decaying substrates, where the activity of one group of organisms is a necessary precursor for the next group in the sequence.

3. DETERMINATION OF MICROBIAL BIOMASS IN FOREST SOILS

Measurement of microbial biomass is a vexing problem for soil microbiologists. Obtaining an estimate of microbial respiration (i.e., O_2 uptake or CO_2 output) is not particularly difficult, but assigning that respiration to various groups of organisms has proven to be a serious challenge. One can readily observe bacterial cells, fungal and actinomycete hyphae, etc. in soil, but there is no way to tell if these are living or dead; and if they are living, whether they are actively metabolizing a substrate or just "resting".

As has been suggested already, a plate count does not reflect, either qualitatively or quantitatively, the soil microflora in its entirety. Some organisms, notably the basidiomycetes, cannot be induced to grow upon agar media even under the most favourable conditions, much less in competition with the numerous fast-growing species always present in soil. The method of preparing a dilution series (shaking a soil with water) and the cultural conditions on a plate of agar (moist, warm, and nutrient-rich) greatly enhance spore isolation, germination and growth. Active microorganisms which are firmly affixed to a substrate, from which they are deriving nutrients, are likely to be discarded with the particles which have settled out from a dilution series or which are floating at the top. Beyond these difficulties, there is the problem of assigning some "average biomass" value to individual microbial cells in order to convert from numbers to weight. Without some detailed knowledge of the characteristics of the population under study, this is likely to be quite arbitrary.

The first real quantitative approach to soil biomass measurement was the agar film method of Jones and Mollison (1948). Previous methods involving stained smears of soil were only semi-quantitative, due to uncertainty as to the amount of soil examined in a dilution, although Thornton and Gray (1934) had partly overcome this problem by incorporating indigo particles of a size and density similar to bacteria. In the agar film method, a known weight of soil is mixed with a small amount of water using a mortar and pestle. This suspension is diluted with molten agar to a known volume, and small amount is placed on a haemocytometer slide. After the agar has cooled, a thin film of known thickness (0.1 mm) has formed, which can be floated onto a regular microscope slide and stained. The size and numbers of cells and hyphae on a number of randomly-chosen fields of the slide are then measured. By multiplying the area of the microscopic fields counted by the depth of the haemocytometer slide, the volume of soil suspension observed is calculated, and the numbers per gram can be obtained using the dilution factor.

The agar film technique was subsequently compared with plate counts by Skinner, Jones and Mollison (1952). "Direct" counts on the film were 40 to 50 times higher for bacteria and 2 to 6 times higher for pieces of fungal mycelium than the plate counts. Furthermore, the two sets of results were poorly correlated in different soils. These workers suggested several reasons that plate counts are underestimates: clumps of bacteria may form a single colony on a plate, competition eliminates some viable organisms, and media selectivity and aerobic incubation exclude many individuals. Inaccuracies in direct counts from the agar film method result from staining of nonviable particles and problems in separating various taxonomic groups. Conversion of numbers to biomass is a problem with both plate counts and agar films, requring the use of an average cytoplasmic density value for microbial tissue together with cell size estimates.

As has been shown by Swift (1973), the numbers of organisms visible in the agar film tend to increase with increasing maceration times, at least up to a a point. A blender or ultrasonic device may give better dispersion and visibility within the film than a mortar and pestle. Jenkinson et al. (1976) estimated volumes of 1.99, 3.38 and 4.96 mm^3 of microbial biomass to be present in 1-gram aliquots of soil using a mortar and pestle, a blender, and an ultrasonic device, respectively. They indicated that an increase in cylindrical organisms (i.e., hyphae) was mainly responsible for the differences. Babiuk and Paul (1970) obtained similar results.

Phenolic aniline blue had originally been proposed as a selective stain for living biomass (Jones and Mollison 1948). Frankland (1974, 1975) found that "ghost hyphae", which lack visible cell components, were also stained and comprised up to 45% of the fungal "biomass" in certain mineral horizons. These ghosts stained a dull purple and were visible under phase contrast, but not bright field microscopy. Other stains have been used which fluoresce under ultraviolet light (Trolldenier 1973). Acridine orange (Strugger 1948) supposedly stains living cells green and dead cells orange, though Casida (1971) showed results casting doubts on the validity of this vital staining characteristic. Babiuk and Paul (1970) described the use of fluorescein isothiocyanate, a protein-selective stain, in quantifying the bacterial biomass of a grassland.

An alternative to preparing an agar film is to filter a known volume of soil suspension and count the organisms appearing on the filter. Hansen et al. (1974), using a microscope equipped with a drawing apparatus, traced lengths of fungal hyphae appearing on a membrane filter onto sheets of paper printed with (9 x 9) cm squares. Although they used a rather complicated statistical length-class method to obtain total hyphal length, Sundman and Sivela (1978) found that a map measurer was faster and reduced error. If a gridded ocular is available, the grid-intersection method of Olson (1950) can be used. Faegri et al. (1977) used a series of homogenization and centrifugation steps to separate bacterial and fungal biomass, and filtered each separately. Filters were stained directly with acridine orange and counted using a gridded ocular. Exceptionally high numbers of bacteria (equivalent to $15 \times 10^{11} \times$ g dry wt. soil) were found in the filtered supernatant. In a subsequent paper (Torsvik and Goksoyr 1978) this group presented DNA values for the bacterial fraction confirming the high counts obtained. Baath and Soderstrom (1980) found that the membrane filter method was faster than agar film, but yielded values 1.1 to 3.9 times lower. They suspected that the filter may reduce visibility, especially for "ghost hyphae", which they found to be especially abundant in agricultural soils. They were, nonetheless, encouraged by the high correlation ($r^2 = .94$) between the two methods for the 10 soils they studied.

It would be convenient if a method were available which did not require the labor of counting cells and measuring hyphal lengths, and the imprecision of converting numbers to biomass. Toward this end, Jenkinson and Powlson (1976a) noted that after a soil is fumigated with chloroform, surviving organisms rapidly convert a fraction of the killed organisms into CO_2. They proposed that the magnitude of this "CO_2 flush" could be used to measure the pre-fumigation soil biomass (Jenkinson and Powlson 1976b). This proposal has attracted much notice, due to its inherent simplicity. Unfortunately, the fraction ("k") of the killed biomass respired by surviving organisms may vary, depending on soil type, the organisms which are killed, and those which survive. When ^{14}C-labelled *Nitrosomonas* cells were lyophilized and added to various soils from the Broadbalk plots at Rothamsted, about 30% of the ^{14}C was released in 10 days at 25°C following chloroform treatment. Subsequent assays of 2 yeasts, 2 sugar fungi, 7 bacteria, and one actinomycete, yielded higher "k" values ranging from 39.7% for a *Clostridium* sp. to 59.7% for *Saccharomyces cerevisiae*; the average was 50.0% (Jenkinson 1976). *Nitrosomonas* appeared to be atypical. Anderson and Domsch (1978a) added ^{14}C labelled sugar fungi and bacteria to 3 arable soils and to the mixed LFH horizons of a forest soil. The average mineralization was 45% for fungi in the arable soils and 40% for fungi in the acid forest soil; values for bacteria were 35% and 26%. They pooled these results, assuming a "typical" 3:1 ratio for fungal and bacterial biomass, to obtain an overall "k" of 0.41. This combined value proved to be highly sensitive to changes in the fraction of bacterial biomass: if it increased from 25% to 45% an overall error of 80% resulted. The variation between arable and forest soils was not discussed.

Some initial studies conducted by Jenkinson's group also cast doubts on the generality of the chloroform fumigation technique, particularly as applied to forest soils. Powlson and Jenkinson (1976) found an acid forest soil in which respiration rates were lower during the 10-day period after fumigation than in untreated soil. Even inoculation did not significantly reduce the "lag phase" for O_2 consumption in this soil. They did not consider that C immobilization might have occurred. They suggested that fumigation releases little decomposable substrate in acid soils, or that decomposition of substrate may be inhibited under acid conditions. Their conclusion that acid soil has a very small biomass seems questionable.

Contradictory results were obtained by Ross et al. (1980), who measured biomass in New Zealand grasslands of varying pH, organic matter, and moisture content. They modified Jenkinson and Powlson's (1976b) calculation procedure slightly, defining the "flush" as the entire period during which respiration in the fumigated soil exceeded the control (anywhere from 6 to 15 days). The "k" factor was assumed to be 0.45 regardless of the time period involved. Whereas Jenkinson and Powlson had actually used unfumigated soil respiration from day 11 to day 21 to calculate the "control" value, Ross et al. (1980) calculated this value from the "most constant" period of respiration in the unfumigated soil. Their four most acid soils had the four highest biomasses; they were also wetter and had higher organic matter contents. Organic matter, moisture, biomass, and acidity all showed highly significant positive correlations, as did measurements of ATP, and mineral nitrogen released during the "flush".

The question of interest here is the validity of chloroform fumigation as applied to a forest soil. There may be unique attributes of forest soil microorganisms which create a net immobilization of carbon after fumigation, unlike the situation in agricultural soils. Alternatively, sampling and maceration of the organic horizon materials of the forest floor could create an abnormally high sustained output of CO_2, particularly if roots are present. If roots are excluded, a significant component of the microflora (mycorrhizal fungi) may be eliminated. More critical studies of the applicability of the chloroform fumigation method of biomass measurement to forest soils are needed.

Anderson and Domsch (1978b) have proposed that the initial respiratory response of soil microbial populations to glucose amendment might provide an even more rapid and convenient method of biomass measurement than chloroform fumigation. Linear rates of CO_2 production for 8 hours were obtained after introducing glucose to soil in solid form (blending it into moist soil with an electric mixer). A comparison with the Jenkinson and Powlson technique produced a high correlation (r = .96). Roots must be eliminated; if present they could act as a glucose sink. This method must be initially calibrated with an independent biomass estimate in order to convert the CO_2 produced into a weight of organisms. A comparison with the chloroform fumigation results suggested that a rate of 1 mg CO_2 h^{-1} corresponds to about 40 mg of microbial biomass-C.

Presumably, any number of enzyme assays might be correlated with biomass measurements in a similar fashion. Nannipieri et al. (1978) showed that CO_2 evolution, phosphatase, urease, and ATP could all be correlated, under certain conditions, with the sum of fungal and bacterial biomass determined microscopically. Whereas ATP and biomass were correlated only with excess inorganic phosphate present, phosphatase levels were correlated with biomass only under P-deficient conditions. Peak CO_2 evolution preceeded biomass production by 18-24 hours, yielding a rather low correlation. Urease yielded the best correlation overall. Domsch et al. (1979) supplied duplicate samples of 6 soils to 4 labs in Germany and Sweden, where various biomass measurements and enzyme assays were performed. All enzyme methods were intercorrelated, a dehydrogenase assay giving the most consistent results. Plate counts were not correlated with biomass measurements made by direct observation, nor were they correlated among the various laboratories. The glucose amendment method of Anderson and Domsch (1978b) yielded excessively high values.

Various components of the microbial cell may be measured, and if their relation to the total microbial weight is known (and fairly constant), a reasonably accurate biomass estimate may be obtained. ATP has already been mentioned. Techniques for soil ATP assays are given by Lee et al. (1971), Ausmus (1973), and Eiland (1979). Cell wall components of bacteria, such as muramic acid, can be measured in soil (Millar and Casida 1970). Similarly, chitin may be assayed as a fungal cell wall component (Swift 1973). There is a group of phycomycetes which lack chitin in the cell wall, so this method would be most useful in woody tissues and other situations where basidomycetes are dominant.

4. ACTIVITY OF THE FOREST SOIL MICROFLORA

Many of the methods for determining microbial biomass discussed in the previous section depend on microbial activity measurements. Respiration as indicated by O_2 uptake gives an estimate of aerobic soil metabolism. CO_2 evolution is also indicative of respiration, although it may include some anaerobic metabolism. Enzyme assays can be used to measure the breakdown of specific compounds such as urea, cellulose, or starch, or they can indicate a broad and poorly-defined spectrum of activity as with the phosphatase and dehydrogenase assays.

Another means of studying microbial activity is by observing successions of organisms appearing on particular substrates. Given a knowledge of the chemical transformations carried out by an organism in pure culture, it is often possible to infer what chemical changes it is causing when it is observed in nature. It is usually true that progressive stages of decay are accompanied both by changing microbial associations and altered proportions of various chemical constituents in the decaying substrate.

4.1. Spatial and temporal variations

As noted earlier, forest soils generally have different microbial populations in different horizons. Timonin (1935) stated that "the microbiological horizons appear to coincide with the morphological horizons." Studies of podzols in Quebec (Gray and McMaster 1933, Gray and Taylor 1935) showed that CO_2 evolution was much higher in the surface organic horizons than in underlying mineral horizons, with roughly a 20-fold difference. Numbers of microorganisms did not show a proportionate decline. Under cultivation, microbial populations increased in podzols but CO_2 production declined. Nitrification was absent in spruce forest soil organic horizons but occurred slowly in the B horizon, suggesting that lower levels of inhibitors were present at depth.

Newman and Norman (1941) pointed out that the variation in CO_2 evolution among the different horizons largely vanishes when expressed on a per gram organic matter basis. However, the horizons differ in responses to organic matter additions, with subsoils tending to show a greater lag period before maximum CO_2 evolution rates occur, and a more rapid decline after the peak. Parkinson and Coups (1963) measured a considerable decrease in O_2 uptake between the F_1 and F_2 layers of a podzol, without a corresponding decrease in fungal biomass. They suggested that hyphae "may have been in a resting state or metabolizing slowly in the undisturbed soil." On a per gram organic matter basis the A_2 was the most actively respiring mineral horizon, even surpassing the organic H horizon. Low moisture contents appeared to limit activity in both the L and A_1 horizons in the field, with water-soluble inhibitors being another possible limiting factor in the A_1. In general, one would expect the organic horizons of forest soil to exhibit higher respiration rates than mineral horizons, either on a dry weight basis or per unit organic matter. As twigs, leaves, bark fragments, etc., decay, sugars and other readily available energy substrates are lost first, leaving cellulose, lignin and other recalcitrant compounds. The remains of a leaf may have been attacked by a number of different microorganisms and passed through the guts of several soil animals before either being reduced to mineral forms or relatively inert humic substances. As litter is fragmented, increased surface area gives more sites of attachment for microorganisms, but there is little available carbon and metabolic rates are corresponingly reduced.

Experimental approaches are also used in the field and in the laboratory. Plastic or metal mesh "litter bags" are used to enclose leaves, small branches, cones, roots, or artificial substrates such as cellulose strips. A number of bags are placed in or upon the forest soil initially, and a series of collections is made through time. Weight loss of the enclosed substrate gives a measure of its rate of decay. Often, concurrent measurements are made of microbial populations or of various chemical constituents in the litter bag contents. It is also possible to make CO_2 evolution measurements directly in the field (Witkamp 1966b).

Laboratory respiration measurements are made upon forest soil under controlled conditions. Waksman and Starkey (1924) indicated that CO_2 evolution reflects soil aeration, moisture content, pH, texture, chemical status, organic matter and its state of decomposition, and the source of organic matter, as well as the number and kinds of microorganisms present. All of these factors have been varied, singly or in combination, by experimental soil scientists. Interactions among these factors sometimes make generalizations difficult. Waksman et al. (1925) suggested that the decomposition of cellulose and lignin in forest soils is largely accomplished by fungi, with bacteria playing a secondary role. In certain soils decomposition is retarded, leading to accumulation of excessive organic material, or "raw humus", at the soil surface. This phenomenon is accompanied by nutrient deficiencies and unfavorable water relations. The formation of organic soil horizons is not an indicator of poor soil conditions per se, however, as it is characteristic of mor soil profiles under coniferous vegetation. The classification of organic soil layers is an interesting part of forest science, and is currently receiving much attention (Klinka et al. 1981).

Spatial variations in microbial activity also occur on a larger scale, often related to local variations in moisture or temperature. Piene and Van Cleve (1978) found that cellulose strips placed in a heavily thinned spruce forest lost weight more rapidly than those in an adjacent uncut forest. They attributed this difference to higher soil temperatures. Forest litter decayed faster in a floodplain than in an adjoining area at 3 m higher elevation, with turnover times of 0.75 and 1.0 years, respectively (Bell et al. 1978). Garrett and Cox (1973) made field CO_2 evolution measurements at three slope positions in an oak-hickory forest, and found highest activity downslope. Medina et al. (1980) also detected higher soil respiration in low-lying compared to drier Amazonian forests, but Reiners (1968) found no differences in cumulative annual releases of CO_2 along an elevational gradient through three Minnesota forest types. Mikola (1960) noted that litter decomposed 40% faster in southern than in northern Finland, and showed that rates were proportional to the mean summer temperature. Schlesinger (1977) calculated a regression equation expressing litter decay as a function of latitude in his extensive review article.

Significant diurnal variations in forest soil CO_2 evolution have been reported, with higher rates either at night (Edwards and Sollins 1973, Medina et al. 1980) or during the day (Witkamp 1969, Garrett and Cox 1973). It is possible, however, that these are caused by tree roots and not microbial respiration. Wetting and drying cycles may have a profound effect on microbial activity.

The flush of CO_2 evolution which occurs upon rewetting a dried soil has been extensively studied in agricultural soils, and its causes debated at length. These include the physical/chemical release of available carbon and ammonium upon drying, death of the drought intolerant portion of the microflora (which are then available for mineralization), transformation of microbial populations from a senescent to a relatively youthful and more active state, and even the physical displacement of trapped CO_2 by the percolating water column. As noted earlier, soil drying alters the composition of the bacterial flora, causing increases in the proportion of spore-forming and *Arthrobacter*-like varieties. Although many bacteria are motile and can presumably escape dry microsites, their movement is comparatively restricted in dry soil (Wong and Griffin 1976). At high water contents, *Pseudomonas fluorescens* is more mobile than *Bacillus subtilis*, which in turn has greater mobility than *Azotobacter* sp. A tendency for *Bacillus* to spread along water films beside killed hyphae of *Pythium ultimum* was noted by these authors, but this could occur only at water contents near saturation. It has been claimed that fungi "can grow through air-filled pores" and presumably are able to translocate water to their growing tips from sites where their hyphae are in contact with water (Griffin 1969). Actinomycetes appear to possess abilities to function at lower water contents analogous to fungi (Williams et al. 1972). Excess water, in contrast, will tend to favor those microorganisms which possess a facultativity anaerobic metabolism, including many bacteria and actinomycetes. Although some fungi tolerate periods without oxygen, their distribution at the top of the peat profile suggests that anaerobic activity is limited (Waksman and Stevens 1928).

Clarholm and Rosswall (1980), by daily sampling of the humus layer of a Scots pine forest, were able to observe rapid fluctuations in the biomass of bacteria in response to rainfall events. They used a modification of the agar film technique to count actual bacterial cells, and in addition grouped them into three size classes. Coccoid forms predominated in the humus during dry periods, but some of these developed into rods, increasing roughly 5-fold in size, after rain and improved growth conditions. Resumption of starvation or drought conditions triggered cell division and resumption of the coccoid form. Thus, changes in biomass were greater than changes in numbers. A rough estimate of the yearly bacterial production was calculated based on the assumption that biomass doubled after an average rainfall event, of which there were 12/year. This gave a value of about $500 \text{ kg ha}^{-1}\text{yr}^{-1}$, similar to a previous estimate of fungal production. It was concluded that bacteria "play a more dominant role in forest podzols than has generally been assumed but their activities are restricted to short periods when conditions favor growth."

Peaks in microbial numbers and activity are commonly observed in spring and fall. This could indicate an association with litter production, root growth, moisture, or temperature fluctuations. Biederbeck and Campbell (1973) found that considerable losses in viable cells occur when temperature is rapidly shifted downward, as often occurs in spring and fall. Upon resumption of favorable conditions, a transient flush in mineral-N production occurs, together with a burst of respiratory activity and increase in microbial numbers. As indicated by Kilbertus et al. (1979), such rapid changes in microbial populations make seasonal variations hard to detect. Their studies indicated that a peak in numbers of microorganisms was found in the spring, with changes most obvious in the top centimeter of the soil. Nicholas et al. (1965) obtained evidence for a "marked, repeated, seasonal increase in mycelium production during the autumn-winter period," which could be seen clearly in the organic and A_1 horizons but appeared not to penetrate to the A_2. They found that one hyphal type, with broad, aseptate hyaline hyphae accounted for most of the change, and tentatively identified it as *Mortierella parvispora*. A fall peak in metabolically-active hyphae was also found by Soderstrom (1979), who used the fluorescein diacetate staining technique. This technique, supposedly selective for actively metabolizing fungi, stains a low percentage (2-5%) of the total observable hyphae. The fall maximum appeared to be associated with increased soil moisture, and declined rapidly when the soil froze. A spring maximum was also observed, which declined as soil moisture was depleted.

Visser and Parkinson's (1975) agar film measurements of hyphal biomass in decomposing aspen leaves indicated that at least 570 kg/ha were produced between June and October. Fungal biomass of leaves just prior to senescence was quite low, yet the same year's crop of litter when sampled on the ground showed a very dramatic, 14-fold biomass increase. Assuming no sampling errors occurred, the fresh litter must have been rapidly colonized by hyphae growing up from the older litter. Rapid changes in hyphal biomass in this aspen forest occurred in spring as well (Parkinson et al. 1979). At the time of snow melt, a sterile dark hypha dominated the litter biomass. However, this fungus was preferentially eaten by grazing collembola, and was quickly replaced by basidomycete hyphae, which were inedible or even toxic for the collembola. Laboratory feeding experiments confirmed this arthropod's food presence and its ability to dramatically alter the distribution of fungal populations.

At least onestudy has attempted to follow seasonal variations in individual fungal species populations. In an oak-birch forest on Long Island, plate counts of microfungi increased from a year-round average of 340,000 g^{-1} dry soil to numbers in excess of 10^6 g^{-1} in spring (Gochenaur 1978). The subsequent rapid decline in summer was also attributed to faunal grazing. *Mortierella* was the only common phycomycete and its abundance closely matched this trend, becoming nearly absent in summer. In all, 30% of the isolates peaked in spring, 20% stayed at constant levels throughout the year, and 35% were absent much of the year (being most likely to be found in spring). A group of cold tolerant fungi, represented by *Oidiodendron* spp., peaked in winter. Basidiomycete sporophores are often observed to be most abundant in the fall (Wilkins and Harris 1946). The conventional explanation for this is that moisture and temperature are favorable. It seems almost certain that seasonal substrate availability also plays a role, with the obvious advantage of fruiting when litter substrates are at a maximum.

It is difficult to trace the impact of any particular environmental variable on microbial activity. Witkamp (1966) used multiple regression equations to study CO_2 evolution from leaf litter, incubated under natural conditions and enclosed periodically in respiration chambers. He concluded that respiration was controlled in order of importance, by temperature, bacterial density, moisture, and number of weeks since leaf drop.

4.2. Leaf litter decay

The simplest model of decay assumes that the rate of decay activity for a given substrate (measured by weight loss, respiration, etc.) is proportional to the amount of substrate remaining. This assumption produces a characteristic exponential decay curve, and allows calculation of turnover rates for decaying litter. Accumulation and disappearance of litter can be modeled, in theory, using simple mathematical equations.

Minderman (1968) pointed out that

litter accumulation cannot be predicted on the basis of known annual litter fall and a fixed turnover value, because each separate chemical component of total litter (sugars, cellulose, lignin, etc.) has its own peculiar decay function. Resistant compounds persist longest, including various polymerized polyphenols and other substances produced by microorganisms. Litter as a total aggregate will not exhibit exponential decay, although individual components might decay exponentially. In support of this, Fogel and Cromack (1976) showed that if 2 years' data were used to calculate needle litter turnover, a higher value was obtained than from the first year data.

Litter decay may be a surprisingly slow process in the forest soil environment. Kendrick (1959) made a simple demonstration of this point. He measured annual litterfall (needles only) in a pine forest, as well as the needle litter weight in the L, F_1, and F_2 horizons. He also obtained the weight of an average needle in each horizon, observing that F_1 needles had lost about 24% of their initial dry weight and F_2 needles had lost 47%. The L layer contained the equivalent of 0.5 years of litterfall, the F_1 layer 2.5 years, and the F_2 layer 7 years. Thus, the average pine needle spent 10 years as recognizable litter, typical of a mor soil profile.

These average values give no indication of the nature of the microorganisms present on litter and their individual decay activities. Certain microbial successions may cause some leaves to decay much more quickly than others.

4.2.1. *Microbial successions*

The succession of microorganisms on leaf litter begins well before leaf-fall. In fact, it may even be traced back to the plant seed in some cases. Many common leaf surface bacteria such as Pseudomonas trifolii may be isolated from seeds. Their numbers increase at seed germination, and they migrate along with the tissues of the growing plant (Last and Deighton 1965). Leaf surface bacteria are common and widespread throughout temperate and tropical regions, sometimes appearing in considerable numbers in air samples, as has been shown for Flavobacterium. Many are washed off and dispersed in rain droplets, but do not usually persist in soil. Most are pigmented, aerobic rods, both Gram-positive and Gram-negative, with few spore formers present. Pigments are thought to increase tolerance to UV light, and perhaps to increase the efficiency of substrate utilization. Holm and Jensen (1972) reported a dramatic increase of yellow pigmented bacteria in a beech canopy in the fall, and it is likely that available substrates increase as leaves senesce. Red and pink pigmented, yeast-like organisms such as Rhodotorula and Sporobolomyces may also be abundant on leaf surfaces, occurring in numbers of up to 3.2×10^7 g^{-1} (di Menna 1959). Unlike true yeasts, the Sporobolomycete yeasts employ forcible spore discharge, and densities of up to 10^6 spores m^{-3} have been found in the atmosphere (Last and Deighton 1965). Other microfungi such as Aureobasidium pullulans and Candida albicans, which are common soil inhabitants, possess yeast-like stages on leaf surfaces. They may at times form virtually pure cultures on plates inoculated with freshly fallen litter. This was noted by Smit and Wieringa (1953) for A. pullulans and by Brandsberg (1969) for a Candida species. A more detailed treatment of this topic is found in Preece and Dickinson (1971).

Leaf surface organisms could be described as primary colonizers, metabolizing the sugars appearing in leaf exudates. According to the scheme proposed by Garrett (1963), these would subsequently be replaced by a second wave of organisms using less readily available leaf substances such as hemicellulose, and cellulose; a third group of organisms would then break down highly resistant compounds such as lignin. The classic example of this sequence is on manure, where the coprophilous fungi which appear in succession can readily be identified by their fruiting bodies. Remacle (1971) interpreted the sequence of bacteria appearing on oak litter in similar fashion. The initial "colonizers" such as Pseudomonas and Flavobacterium, which were undoubtedly present before leaf drop, were common throughout the fall. These were replaced in mid-winter by Bacillus spp. In spring, organisms such as Streptomyces and Cytophaga appeared, which were capable of using cellulose and other less readily available nutrients.

This scheme becomes complicated if internal parasites and saprophytic species are present, as these may greatly limit the availability of nutrients at the leaf surface. Kendrick and Burges (1962) employed methods of leaf washing and surface sterilization to demonstrate the importance of internal colonization in pine litter decay. A parasitic ascomycete, Lophodermium pinastri, invaded living needles and colonized the interior parts, while Coniosporium decayed limited portions of the needle surface. As the leaves senesced, Fusicoccum bacillare and Aureobasidium pullulans appeared, becoming secondary internal and external colonizers, respectively, prior to leaf fall. Coniosporium declined rapidly. After leaf-fall, cross sections through the needles indicated considerable destruction of internal tissues by L. pinastri. A characteristic black ring, easily visible on the needle exterior, demarcated its zone of activity and apparently restricted access to other fungi. However, a third internal colonizer, Desmazierella acicola, gradually gained dominance in the internal succession, replacing both L. pinastri and F. bacillare. These latter two fungi formed large cavities filled with spores after the needles were on the ground for about six months, and ejected the spores to reinfect the living trees. The spores of D. acicola were borne on stalks projecting through the stomata and presumably were adapted for reinfection of fallen needles. When a second crop of needles covered the first, increased moisture allowed two new surface colonizers to gain dominance--Helicoma monospora and Sympodiella acicola. These replaced A. pullulans, which formed pycnidia, sporulated, and reinfected the living trees. They produced abundant conidia and conidiophores which were heavily grazed by mites, springtails and other soil animals. Here, in the F_1 layer, hyphae of a sterile dark fungus and a basidiomycete appeared for the first time as well. D. acicola continued to be active internally, and the combined surface/subsurface attack appeared to effect complete disintegration of some needles. Other needles, which had escaped internal colonization, appeared to form the bulk of the F_2 layer. Decomposition of these needles was quite slow, carried out by a combined attack of the basidiomycete and the sterile dark fungus. Septate hyphae of Trichoderma and Penicillium spp. were also abundant in the F_2. By 7 to 8 years after needle fall, most litter was converted into the remnants of hyphae, faecal pellets, etc. comprising the H layer.

A similar study by Hogg and Hudson (1966) described the microfungal succession on beech leaves. These authors relied heavily upon a "damp chamber" technique (Webster 1956), in which leaves were incubated 2 days under favorable moisture and temperature conditions in closed containers, and subsequently examined under a dissecting microscope. They also suspended leaves just above agar plates to catch ejected spores. These methods allow observation of groups which do not grow readily on agar, particularly ascomycetes and certain Fungi Imperfecti. A great variety of fungi were found to colonize living beech leaves--Gnomonia errabunda and Cladosporium herbarum initially, followed by Botrytis cinerea, Alternaria tenius, and Aureobasidium pullulans as the leaves senesced. Some of these organisms sporulated immediately after leaf fall, while others overwintered and sporulated the following spring. Quite a few persisted in the litter as chlamydospores (A. pullulans) or sclerotia (C. herbarum, B. cinerea) and produced colonies on agar. This made them difficult to distinguish from the true secondary colonizers appearing immediately after leaf fall, such as the ascomycete Mollisina acerina and the imperfect fungus Discosia atrocreas. Many ascomycetes in litter were found to be primary leaf colonizers completing their life cycles. A third group of organisms appeared mostly after the original leaves were covered the next fall, and included a variety of basidiomycetes, imperfect fungi, and 3 more ascomycetes. Simultaneously, *Trichoderma*, *Penicillium*, and assorted Mucorales appeared, which were thought to be "associated with the mycelium of basidiomycetes, such as that of *Clitocybe nebularis* and *Mycena* spp., which were permeating the litter at that time." Hering (1965) worked with a variety of hardwood leaves--oak, birch, hazel, and ash--enclosed in nylon hair nets and pegged to the forest floor. During the first six months after leaf fall, a variety of pycnidial and perithecial fungi were observed forming their distinct fruiting structures on the leaves, although they could not be grown on agar. Up to one year after leaf fall, each tree species had its own unique flora of these ascomycetes and imperfect fungi, whereupon they were replaced by a common flora dominated by *Penicillium*, *Trichoderma*, and assorted Mucorales.

Hudson's (1968) interpretation of these findings gave a very different interpretation of succession than that proposed by Garrett (1963). He cited Chesters' (1949) suggestion that aerial plant parts "arrive at the soil surface very much depleted of nutritional possibilities" as having been subsequently borne out by various workers' observations on decomposing tree branches, trunks, grasses, forbs, and ferns as well as leaves. He claimed that typical "sugar fungi"--phycomycetes such as *Mucor* and *Mortierella*--appear only in the latter successional stages, often associated with basidiomycetes as secondary or tertiary decomposers. Some primary colonizers are host specific, such as *Conosporium* and *Lophodermum pinastri* on pine needles, possessing unique adaptations to the chemical and physical properties of the host substrates. Others such as *Aureobasidium* are more generally distributed, but have complex life cycles enabling them to reproduce in the relatively benign litter environment, while actively growing in the harsher aboveground world. The fallen leaves of particular tree species still retain individual properties which give host-specific species (e.g., *Desmazierella* on pine litter) advantage in some circumstances. Only after a certain degree of decomposition has occurred do the characteristic "soil fungi" gain a foothold.

The distinction between Garrett's (1963) and Hudson's (1968) interpretations of succession is more apparent than real. The growth pattern of sugar fungi--brief mycelial production and rapid sporulation--would make their activity hard to detect with infrequent sampling, particularly if spores were eliminated by washing and surface sterilization methods. Furthermore, studies cited earlier indicate that other organisms, particularly bacteria and yeasts, may be the dominant "sugar organisms" on leaves. A more recent study of aspen litter (Visser and Parkinson 1975) found that leaves caught in a net in the fall were heavily colonized by *Penicillium janthinellum*, which was presumably in a mycelial state, since leaf washing techniques were employed. Various host-specific (e.g., *Pleurophomella spermatiospora*) and "generalist" (*Aureobasidium*, *Cladosporum*) ascomycetes were also found. Soluble compounds such as sugars certainly are important in the initial phase of leaf decomposition, and in some circumstances "typical" sugar fungi may be present. A combination of both Garrett's and Hudson's approaches is useful in understanding other studies of fungal succession on leaf litter (Hayes 1965a and c; MacCauley and Thrower 1966; Watson et al. 1974). Coniferous and angiosperm litter decomposition have been reviewed by Millar (1974) and Jensen (1974) respectively.

4.2.2. Role of soil animals

Soil animals are primary agents of litter decomposition. They may accelerate (or delay) nutrient release by direct feeding upon organic matter and its associated microflora, mixing of soil and litter, improving environmental conditions for microflora, inoculating litter with microorganisms, selective grazing, and maintaining the microflora in an active physiological state (Crossley 1977). They consume a large fraction of litter production, although much of the actual CO_2 evolution from litter is microbial in origin. Macfadyen (1963) estimated that respiration of small arthropods only accounts for 10-20% of litterfall, although the indirect effect in stimulating microbial respiration may be much greater.

Collembola (springtails) and acarids (mites) tend to thrive in fungus-dominated mor humus. Collembola are among the most primitive insects. They show a remarkable cold tolerance and are active at temperatures barely above freezing (Hale 1967). Larger species tend to be fungivores, while smaller ones feed directly on humus. Selective fungal grazing by collembola in early spring may greatly alter fungal species composition (Parkinson et al. 1979). The most abundant order of mites in mor litter is the Cryptostigmata, comprising about 75% of the total acarids (Wallwork 1967). They feed on bacteria and fungi, with immature stages more active than adults. The Mesostigmid mites tend to be predators, while Prostigmids have stylet-like piercing mouthparts for feeding on fungi and roots.

Other animal groups are abundant in certain soils. Earthworms tend to be dominant in creating mull litter profiles, where they greatly speed litter disappearance by pulling leaves into their burrows. In acidic soils these large oligochaetes become rare, but are replaced to some extent by smaller enchytraeid worms. Millipedes may be quite active in the initial stages of litter breakdown. The "aquatic fauna" of the soil includes nematodes, notifers, tardigrades and some of the small oligochaetes. These animals may be active microbial grazers during periods of high soil moisture, and form cysts or other resting forms as dessication occurs. Nematodes are the most numerous soil animals, but most are parasitic on plant roots or predatory on other animals, and do not play a direct role on litter decay.

Since soil animals assimilate only a small fraction of the energy and nutrient content of the litter they consume, much interest has centered upon the subsequent decay of their fecal materials. Litter-derived feces have elevated pH levels, moisture and mineral content. Webb (1977) measured increased nitrogen fixation rates in millipede feces enclosed in litter bags, but did not find that feces/litter mixtures decomposed more rapidly than litter alone. He suggested that particle size plays a major role in feces decay - large feces have a surface volume ratio less than litter itself, and may thereby show reduced decay rates. Grazed oak and dogwood litter tends to retain higher amounts of nutrients than ungrazed litter, perhaps reflecting microbial immobilization and higher cation exchange (Seastedt and Crossley 1980). These findings suggest that animals may promote humification rather than complete degradation of litter. Nagy and Harrower (1980) were unable to find significant differences in decomposition patterns and rates between coprous and non-coprous substrates.

The initial effect of passage through the arthropod gut is for bacteria to be enhanced relative to fungi. Hanlon and Anderson (1980) showed that increased densities of grazing millipedes (2, 4 and 6 animals) increased bacterial standing crops in litter from 1.4 to 5, 8, and 11 mg g^{-1}, respectively. Fungal standing crops declined from 4.6 to 1.6 mg g^{-1} in the 2-animal treatment, but did not decline further with additional grazing pressure. Anderson and Bignell (1980) dissected millipede guts and directly demonstrated that extensive bacterial growth occurs therein. They attributed this effect to favorable growth conditions and a selective enhancement of certain bacteria, coupled with lysis of others. During subsequent decay on millipede feces, bacteria are replaced by fungi - phycomycetes during the first 14 days, then ascomycetes and Fungi Imperfecti (Nicholson et al. 1966). Van der Drift and Witkamp (1960) traced a similar microbial succession on fecal pellets of the terrestrial caddis fly Enoicyla pusilla Burm. Relative to leaf litter, fecal pellets had higher surface area, moisture, and cellulose contents, but lower readily decomposable carbohydrates. Smaller animals, such as Collembola, may feed upon larger arthropod feces, extending the litter comminution process (Poole 1959).

Early studies in which soil animals were excluded from litter enclosed in small mesh bags left little doubt that animal grazing speeds up initial litter disappearance (Crossley and Hoglund 1962, Heath et al. 1964). However, later research revealed that soil animals influence the process of humification as well, acting to retain and concentrate nutrients in the more decayed litter fraction.

4.2.3. Carbon compounds

Litter is chemically heterogeneous, with lignin, cellulose, hemicellulose, pectin, starch, sugars, amino acids, and various aromatic and phenolic compounds among its more common constituents. Ideally, one would wish to know which microorganisms are most active on each compound, and to what extent their decay activities are influenced by environmental variables such as temperature, moisture, acidity, etc. Hayes (1979) remarked that "studies on litter decomposition appear to be largely stuck in the descriptive phase, with comparatively little analysis of the process, while the synthetic phase is at present an unattainable goal somewhere over the horizon. This represents a pessimistic viewpoint; there is much available taxonomic, chemical, and ecological data on litter decay which, when integrated, provides a clear picture of at least the outlines of this process.

Some studies have demonstrated that soluble extracts in leaves from certain tree species inhibit the decomposer flora to varying degrees (Melin and Wiken 1946, Topps and Wain 1957, Knowles and Laishley 1959). The last authors cited found a water-soluble substance in beech leaves inhibitory to fungi, which could account in part for their slow decay relative to maple leaves lacking the inhibitor. This would suggest that a certain amount of leaching would be required for beech decomposition to proceed. A number of studies have shown the importance of the initial "leaching" stage in litter weight loss (Nykvist 1959, Anderson 1973, Howard and Howard 1974, Lousier and Parkinson 1976). This involves the loss of organic substances as well as certain mineral elements, especially K and Na, which are found in solution within the cells of the leaf. Nykvist (1959) found that 22% of the fresh weight of ash litter was leachable, but a much smaller loss (3%) occurred from pine needles. As decomposition proceeded, more water-soluble substance was produced. Artificially leached leaves decomposed more slowly than unleached leaves, indicating that for these species, leachable carbon substances are readily available for microbial decomposition, unlike the situation with beech leaves.

Most leaf structural material consists of large, complex molecules which can be attacked only by extracellular enzymes. Spalding (1977) extracted various extracellular enzymes from Douglas fir needle litter after a short incubation period, during which CO_2 evolution was measured. Cellulase and xylanase activity gave significant correlations with respiratory activity ($r = .58$ and $.44$, respectively). A higher correlation ($r = .71$) was observed with amylase, which is not an extracellular enzyme, but was probably released under the conditions of the enzyme extraction. Spalding suggested that this high amylase activity might reflect utilization of fungal storage compounds. Peroxidase activity correlated with extractable phenolics ($r = .64$), but not with respiration, suggesting that this enzyme might be involved in lignin decomposition. Similar work on extracellular enzyme production in pure cultures of litter microorganisms was reported by Hankin et al. (1976).

Lignin is the most recalcitrant substance in litter, and therefore plays a dominant role in determining decay rates for different substrates. Conifer foliage tends to be higher in lignin than hardwood foliage. Fogel and Cromack (1976) showed that lignin was better correlated with turnover times than C/N ratios for a variety of litter substrates (needles, cones, bark, branches) in a Douglas fir stand. It has been suggested that many aromatic compounds, including certain lignin derivatives, can not be metabolized until an initial energy-requiring step involving reduction of surface carboxylic acid groups has been carried out (Hurst et al. 1962, Hurst 1963). No decomposition could occur without an exogenous source of available carbon.

Successional patterns in the enzymatic activities of litter microflora on alder leaves were demonstrated by Kjoller and Struwe (1980). Microfungi isolated from monthly litter samples by a washing technique were tested on gelatin, starch, pectin, cellulose, chitin, and gallic acid media. The isolates appearing immediately after leaf fall were active on gelatin, starch, and pectin. These included Cladosporium, Phoma, and Aureobasidium. Cellulose utilization was found in virtually none of the initial isolates, but increased to 60% in February. Numbers of gallic acid-utilizing organisms increased concomitantly. By March, Cylindrocarpon, Alternaria, Verticillium and Mortierella were the most common fungi, and a peak in chitinase activity suggested rapid turnover of fungal hyphae. All cellulose active strains also used pectin or starch. Soil immediately under the litter was also sampled, and appeared to contain mostly cellulose- and chitin-utilizing microfungi.

Marten and Pohlman (1942) followed trends in microbial populations, pH, and lignin content after inoculating a variety of air dried, ground leaves with a soil suspension. They found no nitrifying or cellulose-decomposing bacteria in their cultures. The microflora was composed of Gram-negative rods, Bacillus spp., and common fungi such as Penicillum, Mucor, Cephalosporium, Alternaria, etc. An initial pH drop occurred in rapidly decomposing species such as maple, but this was always reversed. High lignin contents retarded decay. The marked pH increase which accompanies leaf decay has also been noted in other laboratory incubations (Broadfoot and Pierre 1939, Nykvist 1959, Sjors 1959). Explanations for the increase include the release of "excess bases" from litter, and the utilization of organic acids.

The activity of microorganisms in pure cultures on leaf material may be rather different from mixed cultures. In Hering's (1967) study, two basidiomycetes (Mycena galopus and Collybia peronata) inoculated on sterile leaf discs were observed to give the most rapid loss of dry weight and lignin. They caused a drop in pH, from about 4.5 to 3.5. Cladosporium herbarum and Aureobasidium pullulans caused virtually no weight loss, while Penicillum thomii and Trichoderma viride were also relatively ineffective in pure culture. No pH changes occurred except in basidiomycete cultures, and no changes in leaf nitrogen content occurred in any cultures. It is likely that basidiomycetes are the dominant litter-decomposing organisms in forest soils, in terms of total dry weight disappearance. Smaller microorganisms may be limited to supporting roles, due to their inability to mobilize sufficient energy reserves to attack large or relatively recalcitrant substrates.

4.2.4. Uptake and release of nitrogen

Nutrient losses from decomposing leaves have received much attention, as it is generally thought that leaf litter mineralization is the major source of nutrients for growing trees. Nitrogen, in particular, has a central role in cell metabolism and growth. However, during initial stages, decomposing leaves represent a nitrogen sink.

The conventional explanation for decreasing C/N ratios in crop residues is that nitrogen is retained while carbon is lost as CO_2, leading to increased nitrogen as a percentage of weight remaining. However, some of the earliest studies of leaf decay in forest soil using litter bags (Gilbert and Bocock 1960; Bocock 1963, 1964), demonstrated that nitrogen increases on an absolute as well as a relative basis, especially during the spring following leaf fall. These scientists tried to explain this in terms of precipitation N inputs, insect frass, loss of male flowers, etc. from the tree canopy. These suggestions were far from satisfactory, merely begging the question of how nitrogen actually became incorporated into the leaves. It was also noted by Bocock (1964) that absolute accumulation of nitrogen was greater in mor, at 40% above initial levels, than in mull soils (10% increase). Subsequent studies confirmed these general trends (Hayes 1965b, Gosz et al. 1973, Howard and Howard 1974, Cromack and Monk 1975, Berg and Soderstrom 1979). Sowden and Ivarson (1974) showed that the increase in the percentage of total N on a relative basis in leaf litter was directly correlated with weight loss, and that absolute amounts of amino acids and hexoseamines increased for about 2.5 years.

Eventually, however, a point is reached at which litter ceases to be a net sink for nitrogen, and becomes a source. One can visualize two separate litter compartments, one which shows net nitrogen immobilization, and the other which shows net mineralization. This latter compartment supplies nitrogen to both the aboveground biomass and to decomposers growing in the nitrogen-deficient litter. If the pool of mineralizing litter is large relative to the pool of immobilizing litter, nitrogen deficiencies will not occur.

The probably mechanism by which nitrogen reaches the fresh, N-deficient litter is by translocation through fungal hyphae. A secondary mechanism could be bacterial fixation of atmospheric nitrogen. The relative magnitude of these two processes is not known. Berg and Soderstrom (1979) demonstrated that the absolute amount of nitrogen in forest litter is directly proportional to its fungal biomass.

The accumulation of nitrogen in litter can be accelerated by applying organic or inorganic nitrogen to the soil (Staaf 1980). It could readily be predicted that increasing the rate of nitrogen supply to leaf litter could increase its breakdown, but that considerable amounts might be required where thick accumulations existed, and that added nitrogen would largely be retained within organic horizons. This has, in fact, been observed in field experiments (Roberge et al. 1970; Adams and Cornforth 1973; Mahendrappa 1978). Increased litter disappearance is not necessarily a desirable goal, in that the fraction of organic soil showing net mineralization may be lost as well as the immobilizing fraction. Aber and Mellilo (1980) reviewed studies demonstrating nitrogen immobilization in fresh litter.

4.3. Root associations

Whereas the microflora of living leaves is considered to be epiphytic or parasitic, the presence of microorganisms both around and within roots may be of direct benefit to the nutrient relationships of the higher plant. Fred and Haas (1919) demonstrated this quite simply by showing that roots infected with bacteria could etch marble to a substantially greater extent than uninfected roots. The formation and decomposition of fine roots is a very dynamic process, difficult to study, and hard to measure quantitatively. Presumably, those organisms active on a living root have a "head start" in breaking down that root after it dies. However, virtually nothing is known about the microbiology of fine root decay (Waid 1974). More information is available on larger roots, but as much of this has been obtained in connection with logging residues, discussion will be deferred to a later section.

Microorganism-root associations are an area of considerable current interest, as noted in the Introduction. Nitrogen-fixing species of the actinomycete genus Frankia have the ability to add substantial quantities of nitrogen to the forest environment, when growing in roots of woody plants such as myrtles and alders. The importance of mycorrhizal fungi in supplying inorganic nutrients to host tree species is well appreciated, but their role in litter turnover has been overlooked, partly due to faulty data interpretation. Recent work with fine root turnover, although shedding little light on actual decay mechanisms, has clearly established the importance of this process in forest nutrient cycles.

4.3.1. The rhizosphere

The region of plant roots, or the rhizosphere, supports high microbial activity. Starkey (1929) reviewed some early work on root-microorganism relationships, and showed his own findings. Plate counts of fungi, actinomycetes, and bacteria increased 57%, 129%, and 195%, respectively, in the root zone of apple trees compared with non-rhizosphere soil. Stimulation of overall carbon dioxide evolution was even greater, at 214%. As the roots of annual plants senesce, bacterial populations decline. Populations associated with perennial plant roots remain high, however, and CO_2 stimulation occurs over longer time periods. Starkey suggested that higher plants must be of considerable importance in determining the "so-called seasonal fluctuations of microorganisms in soil." In 1931, Starkey demonstrated that the zone of influence of plant roots extends out into the soil, at least in terms of increased numbers of bacteria. Perhaps his most interesting work was that published in 1938, where he presented the results of direct microscopic observations of microorganisms in the rhizosphere. He inserted microscope slides vertically into the soil in the field, and planted seeds or seedlings 2 to 3 inches above them. The slides were removed, stained and examined at regular intervals. In the soil itself, the most abundant organisms were small groups of cocci, sometimes in cyst-like masses, associated with clumps of mineral or organic matter. Longer rod-shaped bacteria, actinomycete conidia and filaments, and fungal hyphae were abundant. Development of bacteria around fungal hyphae was often so extensive as to suggest that nutrients were translocated along the hyphae and released at a certain point. He described the growth of microorganisms around roots as "explosive", with the numbers and variety proportional to the degree of root degeneration. Chains of coccoid cells, threads of tiny cells which could not be clearly distinguished as bacteria or actinomycetes and obvious actinomycete filaments were all abundant. Fungi were less noticeably stimulated. Colonization of living roots was quite variable, but a large part of the root hairs and surfaces of larger roots were free from microorganisms.

Lochhead (1940), in the first of a series of studies by Canadian workers, noted that Gram-negative short rods comprise the majority of rhizosphere bacteria, while Gram-positive short rods, coccoid rods, and spore formers are reduced. Predominant soil bacteria such as Corynebacterium are scarce. Lochhead and Chase (1943) developed a nutritional classification scheme, based on ability to grow in basal medium with various combinations of growth factors and amino acids, or with unidentified factors present in soil and yeast extract. They observed that the corynebacteria in general have complex nutrient requirements, fully 57.3% of isolates requiring yeast or soil extract. Organisms requiring amino acids are proportionately greater in the rhizosphere, but most rhizosphere organism do not require growth factors (Lochhead and Thexton 1947). Growth of these amino acid-requiring bacteria is stimulated in tubes containing culture filtrates of rhizosphere bacteria growing on basal medium, indicating that these two groups are closely associated (Payne et al. 1957). The preferential stimulus of amino acid-requiring bacteria in the rhizosphere can also be explained in part by the observation that plants liberate appreciable amounts of amino acids from roots when exposed to drying and wetting cycles (Katznelson et al. 1955).

Other groups of bacteria, such as ammonifiers, denitrifiers, and facultative anaerobes are relatively abundant in rhizosphere soil (Katznelson 1946). The ability of rhizosphere bacteria to reduce methylene blue, proposed as a simple and rapid means of measuring metabolism, was shown to be greatly enhanced (Katznelson and Rouatt 1957a) relative to non-rhizosphere soil. Rhizosphere isolates show much faster overall growth (Rouatt and Katznelson 1957), including a more dynamic response to amendments such as casamino acids (Katznelson and Rouatt 1957b). These effects--ammonifying activity, methylene blue reduction, amino acid utilization--are dependent on the light intensity at which the host plants are grown, suggesting that photosynthesis and translocation of carbohydrates are directly involved in the rhizosphere effect (Rouatt and Katznelson 1960).

Although these observations were made upon crop plants, they were subsequently shown to apply to the rhizosphere of yellow birch seedlings as well (Ivarson and Katznelson 1960). Initial field sampling revealed only a small rhizosphere effect, especially in the organic soil horizon, where it was difficult to exclude root debris and rhizosphere organisms of plants other than birches from the "control" soil. It was observed that forest soils with high organic matter might mask the rhizosphere effect. The effect in birch seedlings grown in the greenhouse was shown to decrease in the period just prior to leaf emergence, then steadily recovered to high levels during leaf development. This recalls Starkey's (1938) observations than rhizosphere bacteria are particularly numerous when roots are decomposing, which presumably occurred after bud break in Ivarson and Katznelson's (1960) study. Katznelson et al. (1962) also compared birch seedlings grown with and without mycorrhizae in the greenhouse. In association with mycorrhizae, total bacterial populations, methylene blue reducers, ammonifiers, and glucose fermenters all showed substantial increases. A decrease in microfungal populations near mycorrhizal roots was accompanied by a shift from a flora composed of *Pythium*, *Fusarium* and *Cylindrocarpon* to active spore-forming fungi such as *Penicillium*, and *Mycelium radicis atrovirens*. It was suggested that root exudation might be more active with mycorrhizae present.

Many studies have focused upon the role of the higher plant in providing root exudates. Rovira (1956) produced a soluble root "exudate" from an acetone extraction procedure and showed that rhizosphere isolates gave a greater overall response to this substance than soil isolates. Rhizosphere bacteria gave a preferential response to the exudate when glucose and amino acids were also present in the medium, while showing a negative response to yeast extract. The exudate selectively stimulated Gram-negative rods when added to non-rhizosphere soil. Slankis et al. (1964) made a careful study of the liberation of ^{14}C-labelled substances from roots of axenic white pine seedlings in solution culture after exposing the above-ground parts to $^{14}CO_2$. After 8 days, uptake of the label was complete, and about 1% had appeared in the nutrient solution. It included various amino acids, organic acids and sugars. Malonic acid was found in highest amounts, with glucose, glutamine, asparagine, and shikimic acid, an intermediate in the synthesis of aromatic amino acids, also abundant. Smith (1977) summarizes much available evidence on the role of tree root exudation in forest ecosystems, including his own findings. Carbohydrates are produced in greater variety and amounts by seedlings, while mature trees produce six times more organic acids per unit dry weight, and release higher amounts of most amino acids. Smith's own field technique involves excising root tips early in the growing season, allowing new unsuberized tips to develop, and returning late in the season to collect exudates appearing in a dilute nutrient solution after thorough surface sterilization. He pointed to certain disadvantages of this method: it is laborious, seasonal changes can not be observed, and the effect of mycorrhizae and other normal root surface microflora cannot be assessed.

Two recent studies have produced direct and indirect evidence for increased root exudation in the presence of a normal bacterial microflora. A study of carbon balance in the root zone of barley plants grown in solution culture (Barber and Lynch 1977) indicated that a greater bacterial biomass was produced in non-sterile culture, than could be accounted for by utilization of carbohydrates released in the absence of microorganisms. During a 6-day period, 3.5 mg carbohydrate was exuded in axenic culture, while 14.17 mg bacteria were produced in non-sterile culture. This is definitive evidence for microbial stimulation of root exudation. By lowering exudate concentrations near wheat roots by frequent changing of the nutrient solution, Prikryl and Vancura (1980) were able to simulate the effect of bacterial uptake of exudates, thereby doubling total amounts of exudate produced.

Other studies of rhizosphere populations have generally confirmed the pioneering Canadian studies. The rhizosphere of citrus trees is dominated by Gram-negative non-sporing rods, with nitrate reducers, methylene blue reducers, gelatin liquefiers, starch hydrolyzers, and amino acid requiring strains relatively abundant compared with populations in nonrhizosphere soil (Rangaswami and Vasantharajan 1962). Oswald and Ferchau (1963) obtained a greater number of bacterial species from conifer rhizospheres (44) than control soil (29) with an approximately equal number of isolation attempts. Skyring and Quadling (1969) submitted 2 sets of 100 isolates from rhizosphere and nonrhizosphere flax soils to 98 different biochemical tests, interpreting their results using principal components analysis, a clustering technique. The control soil isolates belonged to the arthrobacter-coryneform group, while rhizosphere isolates were mostly similar to Pseudomonas, were more likely to show a fermentative metabolism, and were "nutritionally less demanding." They stressed the great dissimilarity between control and rhizosphere isolates.

Some attention has been focussed on nitrogen transformations in the rhizosphere. Nette (1955) reported that denitrifier populations are enhanced 10 to 100-fold in oak rhizospheres, but little production of gaseous N occurs without addition of a carbon substrate. The dominant denitrifying bacteria, which appeared to be related to Pseudomonas and Achromobacter, could also carry out dissimilatory reduction of nitrate to ammonia. Neal et al. (1964, 1968) found that ammonifier populations were increased greatly in the rhizosphere of alder when mycorrhizae were present, while suberized roots had relatively higher populations of nitrate reducers. The effect was similar, but less dramatic for Douglas fir. Precisely the opposite effect was noted by de Leval and Remacle (1969) for mycorrhizal and non-mycorrhizal roots of poplar. This latter study also indicates that rhizosphere bacterial populations change as trees mature. In the poplar rhizosphere, Pseudomonas is commonly associated with young trees, actinomycetes with older ones. Dangerfield et al. (1975, 1978) claimed that ammonifiers were actually less abundant in the rhizosphere of young lodgepole pines. However, they neglected to provide information on conditions and length of sample storage, nor did they suggest whether mycorrhizae were present. The extremely high increases they reported for rhizosphere microbial populations relative to control soils suggests that the particular habitat they studied (a powerline right-of-way) may be atypical. In addition, they sampled large and small roots indiscriminately. For accurate counting of rhizosphere populations, rapid sample preparation is essential.

The relative absence of a rhizosphere effect upon microfungi has puzzled many workers. Harley and Waid (1953) suggested that studies using plate counts probably only demonstrated an absence of fungal spores, since their washing technique showed that a predictable succession of fungi occurred during the development of plant roots. Jackson (1957, 1960) observed that seedling roots could indeed stimulate spore germination, overcoming the general fungistatic effect observed in non-rhizosphere soil. Other root washing studies confirmed Harley and Waid's findings (Peterson 1958; Taylor and Parkinson 1961; Parkinson et al. 1963). However, a comparison of mycelial lengths in control and rhizosphere soil of dwarf beans, using the agar film method, only demonstrated a 2-fold increase in the rhizosphere, and this value was not attained until plants matured (Parkinson and Thomas 1969). Streptomycin and actidione have been used as selective bacterial and fungal inhibitors, respectively, to demonstrate differences between rhizosphere and non-rhizosphere soil respiration (Vancura and Kunc 1977). For sugar beets, 76.7% of the total inhibitable respiration (using both inhibitors) in the rhizosphere was caused by streptomycin, and therefore was attributed to bacteria. By contrast, bacterial respiration was only 17.6% of the total in non-rhizosphere soil. Although fungi may become quite numerous in the rhizosphere under pathological conditions (Timonin 1966), bacteria are apparently dominant in the normal rhizosphere microflora, often in association with mycorrhizal fungi.

4.3.2. Mycorrhizae

The nature and activity of these fungus-root associations has attracted a great deal of interest for many years, yet important questions regarding microbial physiology and taxonomy remain unanswered. The potential for better management of agricultural and forest systems by selection and cultivation of particular mycorrhizal species is conceded to be great, but research in this area is relatively limited. Books are available on the two major kinds of mycorrhizae, the endomycorrhizae (Sanders et al. 1975) and the ectomycorrhizae (Marks and Kozlowski 1973). The former group is extremely widespread on nearly all important crop plants and a number of tree species. The latter group occurs on all members of the Pinaceae and certain other conifers and hardwood trees. Two recent reviews (Maronek et al. 1981, Trappe 1977), which discuss ectomycorrhizae from the point of view of a nurseryman, serve as excellent introductions into the literature. They also cover the numerous studies of the mycorrhizal uptake of inorganic phosphate.

The exchange of carbon between the host plant and fungus is an interesting topic, partly because so much disagreement exists as to its details, and partly because of its potential importance toward an understanding of carbon cycling in forests. The evidence that mycorrhizal fungi are active in litter decomposition and provide plant roots with carbon has been described as "circumstantial" (Mosse 1959). However, it is also difficult to support the view that carbon flow is strictly one-way, from higher plant to fungus. A proponent of this latter view is Harley (1971), who stated that "mycorrhizal fungi are entirely dependent on their host for carbon which they absorb with considerable avidity from direct photosynthetic products." A qualified statement of similar nature was made by Hacskaylo (1973): "In nature, ectomycorrhizal fungi depend primarily upon the roots of their hosts for carbohydrates...certain species of fungi may, however, possess enzymes to hydrolyze cellulose and other complex carbohydrates, but this characteristic does not appear to be widespread." The observations of Went and Slark (1968) on tropical plants express a contrary view, that mycorrhizal fungi "cycle nutrients (organic substances containing minerals or free minerals) directly from organic matter to the living roots with only a minimum of leakage into the mineral soil."

The key work cited supporting one-way flow from host plant to fungus is that of Lewis and Harley (1965). All their studies were performed with excised root tips of beech, some of which were ectomycorrhizal, some uninfected. They showed that mycorrhizal root tips absorbed 2.5 times more ^{14}C-labelled glucose, fructose and sucrose than uninfected roots. In mycorrhizal roots, much of the absorbed sugar was converted into various insoluble storage compounds (mannitol, trehalose, glycogen) by the fungus and stored in its external sheath surrounding the root. Next, the sheath was peeled back and dissected from the excised part of the root but left intact closer to the root tip. If the "naked" part of the root were placed in contact with an agar block containing ^{14}C-sucrose, the same pattern of accumulation could be observed, with insoluble storage compounds appearing, though in lesser amounts, in the fungal sheath. Uptake was only 5% of the rate occurring when a root tip with an intact sheath over its entire length was in contact with the agar block. The further observation was made that whereas mycorrhizal root tips immersed and shaken in ^{14}C-mannitol respired 12% of the absorbed manitol as ^{14}CO , respiration in uninfected roots was only 1% of uptake.

Whereas one might assume that these experiments indicate that the ectomycorrhizal fungus has a strong ability to take up and metabolize external carbon sources, Lewis and Harley came to quite a different conclusion. Their interpretation was that "the fungus absorbs carbohydrates from the host and transfers them into reserve substances peculiar to itself; so maintaining a concentration gradient with respect to host carbohydrate." In a later paper, Harley (1971) cited these findings as indicating a undirectional movement of carbohydrate toward the tips of mycorrhizal roots. In this regard, it would seem that the experimental design precluded the demonstration of movement away from the tips. Also, although synthesis of fungal storage compounds was clearly demonstrated, the notion that a concentration gradient was thereby created can hardly be supported by the data. Nonetheless, this work has been repeatedly cited as evidence that mycorrhizal fungi are wholly dependent upon host plants for their energy requirements.

The other commonly cited evidence for "one-way" movement comes from studies of the carbohydrate nutrition of mycorrhizal fungi grown in pure culture. Many show no growth when provided with cellulose or lignin as sole carbon source, whereas litter-inhabiting basidiomycetes commonly use either of those compounds. Lindeberg (1948) observed that the ability to attack lignin and cellulose is associated with possession of a "polyphenol oxidase" enzyme. She found that the general trend is for mycorrhizal basidiomycetes to possess none, or only small amounts of this enzyme, but that the distinction from the litter inhabitants was not clear: "Within certain genera transitional types are found, which are facultative mycorrhiza formers in the sense that they are able to form fruiting bodies without the mycelium being connected with tree roots...*Lactarius deliciosus*, which is generally looked upon as a typical mycorrhizal fungus, offers special interest by virtue of its strong polyphenol oxidase reaction." Hacskaylo (1965) gave a vivid description of cessation of fruiting body development in *Thelephora terrestris* when its host pine seedlings were covered with a thick cloth to exclude light: "Young sporophores and mycelial masses changed from having a buff to brown, dry appearance to a dark brown, moist collapsed mass, and those on stumps darkened and dried." When the seedlings were uncovered 4 weeks later, fungal development resumed, even on the collapsed sporophore. This very marked dependence on the host plant is still not evidence that ectomycorrhizae are incapable of metabolizing exogenous carbon compounds.

Lamb (1974) showed that a wide range of single carbon sources are used by common ectomycorrhizae isolated from nurseries and plantations; these include glycogen, dextrin, starch and pectin. There is often a considerable lag before active growth commences, suggesting that many previous findings of absence of growth might have reflected insufficient incubation times. Cellulose alone is a poor substrate. However, with glucose added, common mycorrhizae such as *Pisolithus tinctorius* and *Rhizopogon roseolus* show excellent growth on cellulose. Many of these common species had not been previously studied. Lamb (1974) concluded that "the dominant mycorrhiza-formers in nurseries and the unidentified fungi which are widespread in plantations may be less fastidious in their carbon nutrition than better-known fungi and thus perhaps better adapted to survival in the soil in the absence of a suitable host plant."

Mosse (1959) made careful observations on the "extra-matrical" mycelium radiating away from roots infected with endomycorrhizae. She noted that the number of attachment points of external mycelium and the degree of intercellular infection were significantly increased when farmyard manure was added as fertilizer, in comparison with inorganic fertilizers. An ability of the fungus "to accelerate the breakdown of organic matter" was noted. Similarly, endomycorrhizae in the tropics are observed to "weave between and through leaf litter, fallen branches, and heavy, woody fruits", and to be "attached to the dead organic matter by hairs and fine hyphae" (Went and Stark 1968). Wenger (1955) noticed a considerable decrease in mycorrhizal development of pines growing on an area where the A horizon had been stripped off with a bulldozer compared with profiles with intact organic horizons, though he attributed this to decreased sources of infection. Increase of development of mycorrhizae after soil sterilization (Mosse 1959, Skinner and Bowen 1974) could also be interpreted as a nutrient response.

Clowes' (1951, 1954) excellent studies of mycorrhizal root tip development indicated that the host plant's root cap cells are continually produced and sloughed off, even when wholly enclosed within the fungal sheath. He demonstrated that these cells were surrounded and digested by the sheath hyphae. This raised the question of the fate of polyphenols and cellulose in these cells; he concluded that the simplest hypothesis was that the mycorrhizal fungus was responsible for their breakdown as well. Chilvers (1968) later showed electron micrographs confirming Clowes' theory that the root cap cells were decomposed within the sheath.

Levisohn's (1953, 1956, 1960) studies of the role of mycorrhizae in afforestation of an infertile heathland soil are rarely discussed. She introduced *Rhizopogon luteolus*, an ectomycorrhiza normally associated with Scots pine, into pots containing Lawson cypress, which only forms endomycorrhizae. A marked stimulation of root and shoot growth occurred despite the lack of mycorrhizal formation. Introduction of ectomycorrhizae was subsequently shown to stimulate other endotrophic tree species (*Fraxinus*, *Robinia*), and to improve the development of ectotrophic species (*Picea*, *Pinus*, *Betula*) in advance of the actual formation of ectomycorrhizae. In contrast, endomycorrhizae were not observed to stimulate ectotrophic tree species. Levisohn also noted that deleterious effects could occur if mycorrhizal formation was excessively delayed. *Boletus scaber*, although commonly associated with older birches, was extremely slow to form mycorrhizae on young individuals. This exposed the unprotected roots to pathogenic attack by *Mycelium radicis atrovirens*. In explanation of these findings, she suggested that the ectomycorrhizae *Boletus scaber* and *Rhizopogon luteolus* attack organic matter and liberate nutrients in the root zone, which is beneficial, or in the case of the unprotected young birches, detrimental to the developing seedlings.

Host plant nitrogen status is also improved by mycorrhizal infection. Bjorkman originally proposed that high light intensities, and/or low available soil nitrogen and phosphorus, led to accumulation of reducing sugars in the roots and their subsequent infection with mycorrhizae (for references see Harley 1959). Marx et al. (1977) recently tested this theory. Sucrose and fructose contents of pine roots are lowest when high levels of N and P are provided, and significantly less mycorrhizae of *Pisolithus tinctorius* are formed under these conditions. Sucrose contents of short roots measured before inoculation accounted for 85% of the variation in mycorrhizal development. Fructose, however, was not correlated, and they pointed out that the non-reducing sugar sucrose influences mycorrhizal formation, rather than a reducing sugar as Bjorkman proposed. Ratnayake et al. (1978) interpret the role of phosphorus scarcity in terms of root membrane phospholipid contents. Exudation of sugars and amino acids is greatest in leaky, P-deficient roots; conversely, phosphorus inhibition of mycorrhizal synthesis is caused by a "membrane-mediated decrease in root exudation."

Both inorganic and organic nitrogen compounds are transferred through the mycelium of mycorrhizae into host plants (Melin and Nilsson 1952; 1953). Certain amino acids, such as arginine and citrulline, accumulate in plant roots under N deficient conditions. These accumulations indicate a blockage of the "ornithine cycle" of amino acid-synthesis, which is generally alleviated by mycorrhizal infection (Krupa et al. 1973). Some cycling of amino acids between host and fungus may occur. Nitrate is not assimilated by most mycorrhizae and provokes no respiratory response, whereas ammonium absorption is rapid, especially in the presence of added sugars and organic acids (Harley et al. 1954; Carrodus 1966). Bicarbonate is taken up as a "balancing" ion in association with ammonium uptake and is incorporated rapidly into amino acids (Harley 1964).

Other functions of certain mycorrhizal species include enhanced host tolerance of high temperatures (Marx and Bryan 1971) and low temperatures (Maronek and Hendrix 1978). Growth of the mycorrhizal fungus *Cenococcum graniforme* occurs at moisture contents well below the plant wilting point (Worley and Hacskaylo 1959; Mexal and Reid 1973; Theodorou 1978), although it is not clear that this has a beneficial effect on the host plant. Mycorrhizae are intolerant of anaerobic conditions but are not necessarily absent from periodically flooded areas, as shown by their association with willows in a northern wetland (Marshall and Pattullo 1981).

Mycorrhizae give significant protection to the host plant against root diseases (Marx and Devey 1967; 1969; Marx 1972). Zak (1964) proposed four possible mechanisms for disease protection: utilization of surplus carbohydrates, action as a physical barrier to penetration by rhizomorphs, etc., production of antibiotics, and maintenance of a favorable rhizosphere population.

These studies have significant implications for forest management. Mycorrhizae have varying abilities to withstand temperature and moisture extremes, and varying capacities for litter breakdown. It might be possible to enhance the turnover of litter in situations where "raw humus" accumulates by judicious selection of mycorrhizal species. The assumption that a mycorrhiza which is commonly found associated with mature individuals of a particular tree species will be most beneficial to young seedlings is unfounded. There may, in fact, be a succession of mycorrhizal associations formed as trees age, although data is probably not available to test this hypothesis. If endomycorrhizae are commonly associated with litter decay, mixed plantings of endotrophic and ectotrophic trees may result in enhanced nutrient cycling. A site having a mixture of mycorrhizal types may show enhanced cycling due to competition among these organisms. Systematic programs involving isolations of mycorrhizae from many different forest environments are likely to have great practical value.

An organism which persists in the soil must have means of avoiding lysis and milder form of parasitic activity. Thus it is not surprising that basidiomycetes, including mycorrhizal forms, have been shown to possess considerable antibiotic activity (Wilkens 1945; Santoro and Casida 1962; Sasek and Musilek 1967). Whereas the production of antibiotics by an actinomycete would probably indicate parasitic activity, basidiomycete antibiotics could also be used as defence mechanisms, perhaps to establish a sphere of influence for a particular species. Ikediugwu and Webster (1970a and b) observed a phenomenon which they termed "hyphal interference", which involved a "drastic alteration of the permeability of the cell membrane", with loss of hydrostatic pressure, vacuolation, and granulation of the cytoplasm of the affected species. They demonstrated that hyphal interference occurred in a wide range of coprophilous basidiomycetes which showed interference against most lower fungi, and even each other. Basidiomycetes from other soil environments generally exhibited the trait as well, but not lower fungi. Effects were most noticeable at the growing tip of the fungus. These authors did not state their views as to whether antibiotic production was involved.

Gadgil and Gadgil (1971) used a simple experiment to demonstrate that mycorrhizal fungi have an inhibiting effect on litter-decomposing organisms. They laid out twelve one-meter square plots in a Pinus radiata stand, as 3 replicates of 4 treatments. In one treatment, the plot boundary was cut to 30 cm every two weeks, at which time the litter was removed, all roots dug out to 30 cm, and the litter replaced. In the second plot type the boundary was cut, litter removed, the soil dug out without removing roots, and the litter replaced at two-week intervals. In the third plot the boundary was cut and the litter removed and replaced, while in the fourth the only treatment was periodic removal and replacement of the litter. Each of the first three treatments showed a highly significant (p = .001) weight loss compared to the fourth treatment, which differed only in that the boundary was not trenched. Mycorrhizal hyphae, which were abundant in the fourth treatment, disappeared from the three treatments involving trenching. It was concluded that mycorrhizal fungi, "having a biological advantage because they are not dependent on litter for an energy source, become dominant in the litter and suppress the activity of saprophytic organisms. Litter decomposition slows down and conditions favoring mor formation result."

Additional evidence for mycorrhizal inhibition of litter decay has accumulated in two subsequent studies. Laboratory experiments showed significantly lower decomposition rates in pots containing mycorrhizal seedlings than in pots with uninfected plants (Gadgil and Gadgil 1975). This study also reported increased pH and moisture in trenched field plots. However, after experimenting with "simulated clearfellings" in the laboratory, where physical soil changes could be largely controlled, Gadgil and Gadgil (1978) concluded that "the biological changes resulting from clearfelling, including the removal of mycorrhizal root influence, were more important in increasing litter decomposition than the physical effect of the change in climate."

4.3.3. Fine root decay

As indicated earlier, fine root decay has received very little attention. Available evidence suggests, however, that turnover of fine roots is a much more dynamic process than leaf litter decay, and may be of great significance in mineralization and subsequent uptake of nutrients by vegetation.

A recent study is by Grier et al. (1981), comparing a 23-year Douglas-fir stand with a 180-year stand. Their sampling method is to measure fine root biomass in a number of soil cores taken at frequent intervals throughout the year. The difference between "peaks and troughs" of root biomass indicates net production. A fine root biomass peak occurred in the spring, coinciding with the onset of water percolation into soil from the melting snowpack. This peak declined with the beginning of above-ground growth. An autumn peak was also noted, in late August in the young stand, early October in the mature stand. Whereas 30% of the total fine roots were found in the forest floor (organic horizons) of the 23-year stand, the value was 52% in the mature stand. Annual belowground dry weight production (= decomposition) figures were 11820 kg ha^{-1} and 12230 kg ha^{-1}, respectively, for the 23 and 180-year stands. This represented 55% and 69% of the total (above-and belowground) net primary production. Fully 83% of the "total detrital production" (leaf litter plus root litter) occurred belowground in both stands. The authors indicated that turnover values for the entire forest floor calculated from aboveground litter inputs alone would be in error. They noted that "A shift in both the distribution and production of the belowground components of these ecosystems appears to occur as they mature. The structural change is one of increased exploitation of detritus and diminished exploitation of the mineral soil." They suggested that to obtain nutrients from detritus, mature trees must invest more energy to compete with decomposer organisms, and that this greater investment is manifested in increased production and turnover of fine roots, including mycorrhizae.

Although belowground detritus production was higher in the study of Grier et al. (1981) than two similar studies of root turnover (Harris et al. 1977; Persson 1978; 1980), all evidence indicates that it exceeds production of aboveground detritus. It is possible, however, that much of this root turnover represents cycling within the plant/mycorrhiza complex, and that organic compounds are translocated upward rather than being made available for soil decomposer populations. In the tropics, as Jordan and Escalente (1980) have shown, disappearance of leaf litter can be quantitatively related to appearance of new roots. This adds weight to the suggestion of Went and Stark (1968) that organic compounds are, under some circumstances, directly incorporated into root materials via mycorrhizae. Until the roles of mycorrhizae and their associated bacterial flora are clarified, little progress is likely in understanding the dynamics of fine root decay.

4.4. Woody litter decomposition

Considerable decay may occur in standing trees. As in leaf decomposition, this affects subsequent decay on the forest floor. Mangenot (1952) carried out extensive studies of fungal succession on dead deciduous tree trunks in France. The initial stage of saprophytic decomposition was characterized by activity of a variety of lignin-decomposing parasites which persisted after causing tree death; these included Armillaria mellea, Polyporus betulinus, and Phellinus salacinus. In some cases, these decay fungi were sufficiently active to exclude any secondary invasion of lignicolous species. Decay-causing fungi have been extensively studied due to their economic importance, and only a brief discussion of their activities follows.

Pathologists at one time thought that microbial activity in living trees was limited to the heartwood, the central nonliving xylem tissue from which cell contents have been lost, which is impregnated with dark-colored phenolic substances (Shigo and Hillis 1973). However, many microbial infections occur through living tissues, and trees which do not form heartwood are still susceptible to fungal pathogens (Shortle 1979). Wounds exposing outer living cells are colonized by a variety of fungi and bacteria, not all of which are active decay-causing organisms. Bacterial colonization may keep wounds open longer and increase the change of infection by pathogenic fungi (Shigo 1965).

Shortle and Cowling (1978) emphasized the importance of the infected tree's wounding response, involving copious production of phenolic compounds, on the course of fungal succession. Although decay fungi such as Fomes ignarius may initially colonize a wound, only phenol-metabolizing fungi such as Phialophora spp. can make appreciable initial growth. They gradually break down antagonistic phenolic compounds and allow the activity of Fomes to resume. Breakdown of cellulose and lignin becomes more rapid when decay reaches the heartwood. Infection need not occur through wounds. Echinodontium tinctorum basidiospores germinate on small lower branch stubs of hemlock, formed naturally during suppression by upper canopy growth. The fungus may remain dormant for many years until triggered by subsequent injury (Etheridge and Craig 1976). Ascocoryne sarcoides is a fungus which invades through the roots. It is usually non-pathogenic, but may replace Fomes pini as a decay fungus in old-age jack pine stands (Basham 1966). Corticium polygonium, which invades broken aspen branches, may change from a relatively innocuous "stain" fungus to a heartwood-rotting organism in old trees (Etheridge 1961). Aspens are notoriously susceptible to wound-induced decay, particularly by Fomes ignarius. Root rot fungi such as

Armillaria mellea often move upward and cause aspen trunk rot (Basham 1958, 1979).

In wet environments, heartwood may become water-soaked and support an abundant population of anaerobic bacteria. This condition, known as "wetwood", originates in the roots and spreads progressively upward. Methanobacterium may produce internal pressures of methane sufficient to light a flame from a hole bored to the heartwood (Zeikus and Ward 1974). The dominant process is pectin decomposition by Clostridium spp., which attack pectin-containing pit membranes, primary cell walls, and middle lamellae. Acetate, methanol and hydrogen are liberated as fermentation products (Schink et al 1981a and b). These authors found that many species of bacteria in wetwood fix nitrogen. A high percentage of bacterial isolates from decayed living fir trees also could fix nitrogen (Aho et al. 1974). Although fermentative, Gram-negative bacteria are most commonly found within trees, actinomycetes have been reported as well (Blanchette et al. 1981).

The various stages of wood decay are rather complex, involving a great variety of microorganisms. Kaarik (1974) has made a thorough review of the literature on this subject. Woody residues are sometimes produced in large amounts by catastrophic events. Studies have been conducted on decay of timber killed by fire (Basham 1957), wind-throw (Boyce 1929; Buchanan 1940; Davidson and Newell 1953), and insects (Wright et al. 1956; Basham and Belyea 1960; Johnson et al. 1979).

Branch decay is slow in the canopy, where up to 40% weight loss occurs (Swift et al. 1976). Wood decay accelerates on the forest floor, particularly in connection with the activity of soil arthropods. After an initial period when surface feeding invertebrates are active, decay accelerates markedly in conjunction with colonization by wood-boring ants, termites, and beetles. Ausmus (1977) called this process "channelization". She measured 9-fold increases in bacteria and 6-fold increases in actinomycetes during this stage of decay, partly due to transport of microbial cells by invertebrates to the wood interior. Nitrogen accumulates rapidly due to translocation in fungal hyphae and active nitrogen fixation in insect feces. The nitrogen fixing organisms appear to be species of Streptomyces, isolated strains of which may reduce acetylene to ethylene. The general trend of declining wood pH is temporarily reversed during channelization. Fungal rhizomorph development and colonization by annelids first occurs during this stage.

Wood decay generally involves accumulation of organic acids and increased moisture. As is true for leaves, absolute nitrogen amounts also increase. At some point a "critical level" of nitrogen is reached, which is lower for slowly-decomposing woody tissues than for leaves (Berg and Staaf 1981). Beyond this point, release of nitrogen occurs in proportion to total weight loss. Aber and Melillo (1980) showed that the initial rates of nitrogen accumulation for either leaves or wood were proportional to weight loss.

Fungi which decay wood must make highly efficient use of nitrogen, including "a dynamic and continuous process of autolysis and reuse" of the nitrogen within their own tissues (Cowling and Merrill 1966). The relative importance of fungal translocation and nitrogen fixation during the accumulation phase has been debated (Ausmus 1977; Swift 1977), but these processes are conceded to be far more important than passive inputs in rainfall and throughfall leachates. Fungal hyphae are enriched with nitrogen compared to the woody substrate in which they are growing, and this is true for other elements such as potassium, magnesium, and phosphorus (Cromack et al. 1975, Swift 1977). Calcium is taken up in very large amounts by fungi and excreted as an insoluble oxalate salt, which is thought to be the major waste product of fungal metabolism (Cromack et al. 1977).

The distinction between white-rot fungi, which break down both cellulose and lignin, and brown-rot fungi which decompose only cellulose with limited cleavage of lignin methoxyl groups, has long been appreciated (Bray and Andrews 1924). Kaplan and Hartenstein (1980) have reviewed some more recent studies and reported on work with synthetic, ^{14}C-labelled lignins. The mechanism by which brown rot fungi degrade cellulose in wood--"rapid depolymerization at low weight loss"--has attracted considerable attention, especially given the sparse growth of these organisms on cellulose as a sole carbon source (Highley 1980). One proposal is that cellulose cleavage is nonenzymatic, and that brown rot fungi use a combination of hydrogen peroxide and iron to effect a physical attack on the molecule (Koenigs 1974). Due to the selective attack on cellulose, brown-rotted wood retains much weight and volume over long time periods. This is particularly characteristic of conifer logs. Wood infected with white rot fungi decomposes relatively quickly.

The aromatic compounds such as vanillin, ferulic acid, etc., which are released during lignin decomposition are broken down by a surprisingly wide variety of fungi and bacteria (Henderson 1960, 1963) as well as actinomycetes (Sutherland et al. 1981). Although synthetic lignins are stable under anaerobic conditions (Hackett et al. 1977), it has recently been shown that lignin breakdown products decompose readily in methanogenic cultures (Healy et al. 1980). Phenolic degradation products of lignin need not appear as CO_2 or CH_4 in nature. Considerable evidence suggests that oxidative polymerization of these compounds leads to humus-like materials (Kumada et al. 1961). This process is associated with fungal laccases (Fahraeus 1954; Law 1959) and the phenoloxidases of streptomycetes and bacteria (Sorensen 1962; Kuster 1963), and appears to occur under unfavorable conditions or restricted growth.

The production of large amounts of woody litter, both above-ground and below-ground, is a feature of many clear-cutting operations. Recent trends toward increased biomass utilization are reducing the amounts of slash, and even stumps, remaining after forest clearing. Extensive work on slash decay, including the microorganisms responsible, their environmental tolerances, and rates of activity, has been carried out in both the U.S. and Canada; much of this is cited in Aho (1974). The work of Spaulding and Hansbrough (1944) should be mentioned; it represents many years' research in forests of the northeastern U.S. Moisture, temperature, and wood decay resistance are primary factors influencing slash decomposition. Either waterlogging or insufficient moisture retards decay. Debarked wood, especially white pine, may dry excessively and pose a fire hazard. This is often noted in small twigs which are described as "case-hardened". Partial cutting creates more favorable conditions for slash decomposition than clear-cutting, where excessive drying and temperature fluctuations become inhibitory. Spaulding and Hansbrough gave extensive lists of slash decay fungi, including some which cause heart rots and persist in stumps (Armillaris mellea) or defective logs (Fomes applanatus, F. pini). They shared the opinion of many authors that fruiting by these fungi in the slash did not provide a hazard to young trees, nor to existing trees, provided that care had been taken in the logging operation to avoid knocking off large sections of bark or branches.

Highley and Kirk (1979) suggested that slash fungi do not usually cause heart rots due to their intolerance of low O_2 and high CO_2 levels in the living tree, and in some cases an intolerance of phenolic compounds produced during the host wounding response. Conversely, heart rot fungi do not persist in slash, where they lose the advantage gained by adaptation to conditions in the living tree, and are unable to tolerate wider fluctuations in moisture or temperature. The work of Loman (1962, 1965) is notable in showing that certain fungi, especially Lenzites saepiaria and Peniophora phleboides are tolerant of high temperatures in the upper levels of slash, while the fungi present in lower levels can sometimes invade the upper slash in cooler weather. Childs (1939) made extensive observations on the activity of *Lenzites saepiaria* with respect to moisture variations in Douglas-fir slash. Although basidiomycete fungi are the dominant slash-decaying organisms, associated bacteria increase decay rates. This was demonstrated in laboratory studies by Blanchette and Shaw (1978), who essentially repeated an experiment performed by Schmitz in 1919.

There is an extensive literature on stump decay as well. The wounding response of the living cells at the freshly cut stump surface creates a strong selective pressure upon potential colonizing organisms. Meredith's (1959, 1960) studies of the interaction of the pathogenic root rotting fungus *Fomes annosus* with other stump colonizers are classics. *F. annosus* can grow rapidly down through the stump and outward in the lateral roots, infecting neighboring healthy trees through their roots. If a non pathogenic fungus such as *Peniophora gigantea* colonizes the stump initially, growth of *F. annosus* is entirely checked. Artificial inoculation with *P. gigantea* is an effective means of decreasing the infection potential of *F. annosus* (Rishbeth 1963; Boyce 1966; Ginns and Driver 1970). Alternatively, cutting can be timed to occur when environmental conditions are unfavorable for sporulation and/or growth of this pathogen (Rishbeth 1951; Yde-Andersen 1962; Gooding et al. 1966). Although *F. annosus* can persist for many years in large stumps, it is gradually replaced by a variety of common soil fungi, such as *Trichoderma viride*, which enter through the roots and spread slowly upward as more favorable moisture and nutritional conditions are created by advanced decay (Meredith 1960). Unfortunately, in some northern conifer forests, *Armillaria mellea* may replace *F. annosus* earlier during decay, and can spread to cause serious root rot in nearby trees as well (Morrison and Johnson 1978). *Armillaria mellea* was the dominant root-rotting organism found in a study of young conifer seedlings in northern Ontario (Whitney and Myren 1978). A ponderosa pine forest has been studied where a single clone of *A. mellea* has apparently persisted and spread for at least 460 years, with repeated outbreaks triggered by timber harvesting operations (Shaw and Roth 1976).

Harvey et al. (1976) noted that decayed wood is an important substrate for the formation of ectomycorrhizae. They subsequently found that the moisture retention capacity of decayed wood makes it increasingly important as a reservoir of biological activity in dry summer months. Ectomycorrhizae survive in rotting wood under conditions which are lethal in the mineral soil (Harvey et al. 1978; 1979). This has led these workers to suggest that woody logging residues be carefully managed, with a view toward maintaining the capacity of the soil to support organisms favorable for tree growth (Larsen et al. 1980).

5. Nitrogen transformations

Nitrogen is frequently observed to be a limiting factor for tree growth. Excessive accumulations of nitrogen poor litter are found in many forest stands, particularly even-aged conifer stands. Much of the available nitrogen is immobilized by litter decay microorganisms, creating deficiencies in the above-ground woody vegetation. Even where litter decay is not inhibited by nitrogen shortages, tree growth may show a positive response to nitrogen fertilization.

Considerable releases of mineral nitrogen into drainage waters may occur following tree harvesting. Much research effort has been expended in documenting these losses and elucidating the mechanisms involved. Microbial processes such as mineralization, immobilization, and particularly bacterial nitrification largely determine the timing and magnitude of these post-harvest nitrogen losses.

On the other hand, microorganisms may add significant amounts of nitrogen to the forest ecosystem through bacterial nitrogen fixation. The highest gains are observed where bacteria are growing in association with the roots of woody plants, forming characteristic nodule structures. These symbioses are of mutual benefit to microbe and plant. The former organism obtains a reliable energy source in the form of photosynthetically fixed carbon, while allowing the latter organism to obtain its nitrogen requirements from the atmosphere.

5.1. Mineralization and immobilization

Mineralization of nitrogen is the production of inorganic forms such as ammonium and nitrate from organic nitrogen compounds. If litter turnover is in steady state, the nitrogen content of annual litter production (including leaves, branches, and roots) determines annual potential mineralization. However, much of the organic nitrogen in litter never appears in mineral form, being incorporated directly into microbial biomass. Incorporation of organic-N compounds may even occur in woody biomass via mycorrhizal-root associations (Melin and Nilsson 1953). Thus it is not certain to what extent the high levels of root litter production measured by Grier et al. (1981) are accompanied by the appearance of mineral nitrogen in forest soil. Obtaining an estimate of nitrogen mineralization rates in the laboratory is straightforward, but one can never be certain that similar conditions prevail in the field.

Many different techniques have been used in calculating nitrogen mineralization in forest soils. Duchaufour (1954) added peptone to samples of acid mull and acid mor humus, and found that it could be recovered almost quantitatively as NH_4^+ after a 15-day incubation at 30°C. Most ammonification occurred during the first two days. The total NH_4^+ produced was about equal to the sum of the added N and the NH_4^+ produced in unamended samples, although slightly more NH_4^+ was produced in the mor humus. Faille (1975) studied the changes in nitrogen mineralization occurring in mature forests where tree fall created small clearings. Total mineral N produced in six-week laboratory incubations of unamended soil was generally equal to or greater than amounts produced in one-year field incubations, in open, sunken boxes. This discrepancy was especially great in mull humus, where high production of herbaceous litter in areas receiving full sunlight led to net nitrogen immobilization, at least during the winter. Remacle (1977a) buried gelatin film in spruce and beech soils, obtaining nitrogen losses of 50% and 64% per year, respectively. By assuming that concentrations of organic nitrogen in litter turned over at a proportional rate, he estimated litter-N mineralization rates of 10 kg ha^{-1} yr^{-1} and 32 kg ha^{-1} yr^{-1} in the two soils. These values were less than a third those obtained in laboratory incubations. Glavac and Koenies (1978) excavated large blocks of forest soil from spruce and beech forests and buried them in nearby open fields, thereby "simulating" the effects of clear-felling. Other blocks were excavated but returned in place. The simulated clear-felling increased mineral-N production in the spruce soil from 31 to 94 kg ha^{-1} for six-week incubations, while the beech soil was relatively unchanged, remaining at 35 kg ha^{-1}. Other studies have shown that counts of ammonifying and nitrifying organisms are not correlated with laboratory N mineralization rates (Ross and Bridger 1978), and that litter nitrogen content is not well correlated with mineralization and uptake of nitrogen by Douglas-fir seedlings grown in pots (Youngberg 1978).

All these studies share a common flaw, that measured rates may not relfect actual N mineralization in the undisturbed soil profile. It is certainly possible that when roots and associated mycorrhizae are severed during sampling, rates are altered. Keeney (1980) suggested that organic horizons be excluded from calculations of net mineralization. He pointed out that litter organic-N content increases with time in the field, whereas laboratory incubations suggest a net release of mineral-N. Apparently he failed to make a distinction between the field situation where litter is added and disintegrated simultaneously, and the lab situation where only disintegration occurs.

It is worth pointing out, however, that if mineral-N is only translocated from decayed to fresh litter, it is not made available to the plant. Competition between roots (with or without mycorrhizae) and litter decomposing organisms is likely to be of considerable importance.

Incubations of soil with fresh litter yield predictable results: a tendency for net N immobilization to occur, at least initially (Fenton 1958). Sowden and Ivarson (1959) observed that amino acids increase during the immobilization phase, as do galactose- and glucoseamines, indicating incorporation within microbial cell walls. Bernier and Roberge (1962) found that C/N ratio does not always indicate potential immobilization. Decaying mosses, despite an initial C/N ratio of 35 to 59, mineralize nitrogen immediately. Jones and Richards (1977) noted that lime promotes immobilization when pine needles and NH_4^+ are added to podzol soil, as bacterial populations increase substantially. These laboratory studies show a clear analogy to field studies discussed earlier, where absolute nitrogen accumulations occur in leaf and wood litter until some critical value is attained.

Immobilization of nitrogen is not restricted to biological processes. Ammonium added to sterilized raw humus may be partly incorporated into a non-hydrolyzable fraction (Nommik 1970), especially if pH is increased. This process may involve formation of phenolic-protein complexes, observed by Handley (1961). Studies with ^{15}N-labelled compounds indicate a rapid exchange of labelled for unlabelled N, which is an order of magnitude greater than actual immobilization (Chu and Knowles 1966; Knowles and Chu 1969; Von Praage and Brigode 1973; Knowles 1973). It would seem that when organic-N compounds are added to humus, the apparent "rapid mineralization of NH_4^+" may partly reflect a displacement of humus-NH_4^+ groups, accompanied by binding of the organic compounds without degradation. Jones and Richards (1978) found that periodic burning of a eucalyptus forest increased the incorporation of added $^{15}NH_4^+$ in non-hydrolyzable forms, with greater incorporation in hydrolyzable forms in an unburnt pine soil humus. They interpreted this as indicating different patterns of fungal activity, but strictly physical/chemical processes might also be important.

Changes in mineralization/immobilization patterns in relation to age and other stand characteristics are currently receiving much attention. When conifers are first established on an area, initial growth is often excellent. Fisher and Stone (1969) suggested that "the conifer rhizosphere mineralizes or otherwise extracts some fraction of the soil N that had been resistant to microbial action under the previous vegetation." As the stand matures, nitrogen is progressively immobilized in the organic matter accumulating at the surface. Surprising site-to-site variation is found, with maximum accumulations on poor soils such as deep sandy podzols (Lamb 1975). Slow litter turnover on these poor soils, as reflected in low mineralization rates in laboratory incubations, can be related to the "needle nutrient withdrawal rate." Nitrogen is translocated from older needles into younger needles, creating an independent nitrogen cycle within the tree itself. On poorer soils, nitrogen withdrawal is intensified and fresh needle litter is increasingly depleted of nutrients (Lamb 1975; 1976; Turner 1977). This litter, in turn, ties up a higher proportion of the total available N in the soil. Productivity of the second generation of pine trees declines noticeably on these sites. These "tight" nutrient cycles on poor soils are characterized by high retention of atmospheric inputs, and special means of extracting nutrients from "intractable" sources, i.e., abundant mycorrhizae (Miller et al. 1979). An excellent review of these trends is given by Gosz (1981).

5.2. Nitrification

A disproportionate amount of attention has been given to autotrophic nitrification in forest soils, primarily because of findings that large nitrate losses can follow forest clearing under some conditions. The organisms responsible include several genera of chemoautotrophic bacteria, which obtain energy from the oxidation of ammonium to nitrite (e.g. *Nitrosospira*, *Nitrosomonas*) or nitrite to nitrate (e.g. *Nitrobacter*) and carbon from atmospheric CO_2 (Belser 1979). They are therefore not dependent upon forest litter as an energy or carbon source. It has long been recognized that nitrification activity is very limited in coniferous forests. Gray and Taylor (1935) found no nitrate production in spruce soil A horizons, while limited activity in the B horizon indicated a reduction in "inhibitory substances" present at the surface. Rice (1964) and Rice and Pancholy (1972) were particularly active in searching for inhibitory substances, and proposed that mature ecosystems in general tend to inhibit nitrification as a way of avoiding NO_3^- leaching losses. However, many mature forests have active nitrifying populations (e.g., Ellis 1974), and different trees within the same forest create varying degrees of inhibition (Lodhi 1978). Acidic, nutrient poor tropical soils strongly suppress nitrification even if the root mat is severed from the trees (Jordan et al. 1979), while in more productive rain forests a gradual increase in nitrification activity may occur during stand development (Lamb 1980). Nitrification in forested ecosystems has been recently reviewed by Robertson (1982).

Research in Canada (Chase and Gray 1957; Chase, Corke and Robinson 1967; Corke 1958) demonstrated that applications of limestone to an acidic, second-growth beech-maple forest could induce active nitrification, and increase the populations of autotrophic nitrifying bacteria. Phosphate addition further enhances the numbers and activities of these organisms. It is not possible to specify a pH limit below which nitrification is absent. This seems to vary from soil to soil. Bollen and Wright (1961) measured high nitrate production in the L and F_1 horizons of a virgin Sitka spruce stand, despite a pH of 5.11. Young red alder and ponderosa pine stands had high soil nitrate concentrations initially which declined to zero during incubation. Even quite acidic alder stands sometimes exhibit significant nitrifying activity (Bollen and Lu 1968). Lack of nitrifying activity in Florida soils is attributed to a combination of low pH, low nutrients, and poor aeration (Pritchett et al. 1959). Webber and Gainey (1962) found active nitrification in some bottomland soils at pH 4.0. They noted that nitrifiers isolated from there soils were inactive in liquid culture below pH 6.0. Sarathchandra (1978) found that the lower pH limit for nitrification in his perfusion apparatus was 4.3, while Walker and Wickramsinghe (1979) found ammonium-oxidizing bacteria common in the pH 4.0 to 4.5 range. Rennie and Schmidt (1977) compared fluorescent antibody (FA) and most probable number (MPN) counts for *Nitrobacter winogradskyi*, introduced into 5 soils ranging in pH from 4.7 to 7.2. Whereas FA counts were all similar (10^5-10^6 g^{-1}), highly reduced MPN counts (10^1-10^2 g^{-1}) were found in the pH 4.7 soil. The MPN counts averaged 100-fold lower than FA counts in the neutral soils. Population increases measured by the 2 methods were similar, suggesting that the MPN technique only measures a small fraction of nitrifying bacteria present in acid soils.

The Hubbard Brook experiment could be regarded as a field study in nitrification. A 15.6 ha beech-maple forest was cut in winter, all slash levelled to a height of less than 1.5 m, and left in place. Herbicide was applied the following June to inhibit vegetation regrowth. Streamflow nitrate-N concentrations began to rise before herbicide application and eventually peaked at 50 mg l^{-1}. The relatively large net loss of nitrogen (52.8 kg ha^{-1} yr^{-1}) was explained primarily by "cessation of uptake of nutrients by plants," with increased mineralization (higher temperature) and "release from inhibition" of nitrification playing secondary roles (Bormann et al. 1968). Increased populations of *Nitrosomonas* (18-fold) and *Nitrobacter* (34-fold) were observed on the cut-over area as compared with the control watershed (Smith et al. 1968).

Elevated nitrate levels and nitrifier populations are certainly not observed in all clear-cut areas. Vitousek and Melillo (1979) have summarized a number of studies where nitrate losses from cut-over watersheds have been recorded. They noted that an imbalance between nitrogen mineralization and vegetation uptake is usually temporary, and that annual mineralization always greatly exceeds annual nitrogen loss, at least 40-fold. Vitousek et al. (1979) reported results from small forest plots which were trenched to eliminate plant uptake. Lysimeters were installed to monitor leaching losses of NH_4^+ and NO_3^- to groundwater. Pine sites around the United States generally show a lag before NH_4^+ production occurs with NO_3^- production occurring only after a long lag period. Oak sites show immediate NH_4^+ production. A number of hypotheses were suggested to explain these findings, including very slow growth of nitrifier populations, or competition between decomposers and nitrifiers for a limiting element such as phosphorus.

Johnson and Edwards (1979) report findings from an experiment where a stand of tulip poplars were stem-girdled and left standing in place, again in an effort to eliminate plant uptake while minimizing soil disturbance. Nitrate losses were 25.4 kg ha^{-1} yr^{-1} from the girdled plot, 0.15 kg ha^{-1} yr^{-1} from the control. In laboratory experiments, added sucrose increased CO_2 evolution while decreasing N mineralization and nitrification. They inferred from this that N is a limiting element and heterotrophic demand for NH_4^+ regulates nitrifier activity. As indicated earlier, other interpretations might be offered, such as available carbon limitation or limitation by another mineral element. Their observation that aboveground leaf production and photosynthetic activity continues at a near-normal rate for at least 2 years after tree girdling is interesting. This suggests that internal cycling of carbon, and other elements, may make aboveground plant tissues relatively independent of nutrient uptake. Similarly, they found a surprisingly small decline in fine root biomass after two years, indicating that a large reserve of belowground energy and nutrients is maintained. Patterns of internal translocation of nutrients appear to be a neglected area of the forest nutrient cycle. There may well be a considerable upward movement of energy and nutrients stored in root tissue in the spring, and a downward movement of substances reabsorbed prior to leaf senescence in the fall. Such patterns might extend out into the soil via seasonal trends of root uptake and root exudation, affecting heterotrophic activity.

Other groups besides the autotrophic nitrifying bacteria may be active in producing soil nitrite and nitrate. Methane oxidizing bacteria have been shown to produce varying amounts of nitrite from ammonium. Romanovskaya et al. (1977) proposed that this can serve as an alternative to methane oxidation as an energy yielding reaction, but other studies (Dalton 1977; O'Neill and Wilkinson (1977) do not support this interpretation, and show relatively insignificant nitrite production. Verstraete (1981) has reviewed these studies.

In contrast, heterotrophic nitrification by Aspergillus flavus is a well-established phenomenon. Schmidt (1954) reported the isolation of a nitrifying strain of A. flavus and subsequently showed that 16 of 18 actively nitrifying fungal cultures (from 978 original isolates) were members of this species. The mechanism of heterotrophic nitrification differs markedly from autotrophic nitrification, in that NO_3^- is produced only after cessation of active growth. Organic nitrogen compounds such as aspartate are used. Nitrification is inefficient, being accompanied by 10-fold greater ammonification. A shift from a cytochrome-type respiration to a flavoprotein type suggests that nitrification contributes to the maintenance energy of the resting mycelium (Van Gool and Schmidt 1975). Measureable heterotrophic nitrification has been reported in neutral soils (Odu and Adeoye 1970). Remacle (1977b) found that nitrate production by a Penicillium sp. in nutrient-poor continuous culture is detectable at pH 5.1, and increases under more alkaline conditions. Heterotrophic nitrification by fungi is one possible explanation for the production of small amounts of nitrate in acid forest soils where no detectable autrophic nitrifying activity exists.

5.3 Denitrification

Denitrification is defined as the production of N_2 and gaseous oxides of N from nitrate (NO_3^-) or nitrite (NO_2^-). The process is abiological or biological. Abiological denitrification which requires high NO_2^- and low pH is generally low and insignificant (Wollum and Davey, 1975). Biological reactions are mainly responsible for returning the N_2 to the atmosphere thereby completing the N cycle.

Many common microorganisms are capable of mediating biological denitrification by using NO_3^- instead of O_2 as terminal electron acceptor in respiration, forming mostly nitrous oxide (N_2O) and nitrogen (N_2). The process is important from a soil fertility viewpoint in that it results in a permanent loss of available nitrogen from the soil. Also of concern is the accumulation in the atmosphere of N_2O which is involved in reactions leading to the depletion of stratospheric ozone (Crutzen, 1970, 1976). Recent reviews on denitrification were done by Knowles (1981, 1982). Rapid denitrification is generally favoured by anoxic, warm near neutral organic soils. Denitrification in apparently well "aerated" arable soils is presumed to occur in anaerobic microsites (Wollum and Davey, 1975).

Information on denitrification in forests is almost non-existent. Because of the dynamic nature of N transformations it can be dangerous to dismiss denitrification as insignificant in forest soils merely on the grounds that nitrate levels are low. Evidence that denitrification may be occurring in acid forest soils at least at low levels was presented by Overrein (1969) when he detected $^{15}N_2$ in trace amounts from plots tested with urea-^{15}N. Keeney (1980) has pointed out that while the forest soil with relatively high levels of soluble organic matter offers an excellent environment for denitrification it cannot occur without nitrate and little nitrification normally occurs in unamended systems. Increased soil nitrate concentration resulting from increased nitrification and water levels (which enhances anaerobiosis) following clear-cutting of some forests may accelerate denitrification (Vitousek, 1981). Physical and biological alteration of the forest environment through other management practices such as slash-burning and use of chemicals (fertilizers, herbicides etc.) could potentially influence losses of N through denitrification. Clearly more research should be directed towards denitrification in forests to fill gaps in our knowledge and to aid in developing better management techniques.

5.4. Nitrogen fixation

Interest in biological nitrogen fixation in the forest environment has grown tremendously in recent years. Enhanced nitrogen fixation in today's intensive forest management may not only be economically attractive, but is also energy efficient and environmentally benign. For a detailed discussion of the potentials and implications of nitrogen fixation and other root symbioses in forestry, the reader is referred to a recent paper by Fortin and Carlisle (1982).

In forests, nitrogen can be fixed by free-living microorganisms or by those living in a symbiotic relationship with higher plants. Fixation by free-living organisms is generally low, in the order of 1–5 $kg\ ha^{-1} yr^{-1}$ (Wollum and Davey, 1975) but under certain conditions may reach 10–50 $kg\ ha^{-1} yr^{-1}$ in temperate forests (Jurgensen and Davey, 1971; Richards, 1973). In contrast nitrogen-fixation by symbiotic organisms can be as high as 300 $kg\ ha^{-1} yr^{-1}$ (Fortin et al. 1979). Table 1 compares the rates of symbiotic nitrogen fixation by legumes and non-legumes in the field.

Table 1. Rates of nitrogen fixation by legumes and non-legumes in the field*

LEGUMES (*Rhizobium* symbiont)	Nitrogen fixation rate (kg ha^{-1} $year^{-1}$)	Reference
Glycine max (Soybean)	57 - 94	Burns & Hardy in Fortin *et al* 1979
Apios americana (Groundnuts)	47 - 91	"
Pisum spp. (Garden pea)	85	"
Lens esculenta (Lentil)	85	"
Vicia spp. (Vetches)	85	"
Trifolium spp. (Clovers)	105 - 160	"
Medicago sativa (Alfalfa)	128 - 300	"
Lupinus spp.	150	"
Acacia spp.	270	"
NON-LEGUMES (*Frankia* symbiont)		
Alnus rubra	100 - 300	Fortin *et al* 1979
A. crispa	62 - 157	"
A. rugosa	79 - 150	"
A. incana	50	"
A. glutinosa	12 - 30	"
Casuarina spp.	50 - 200	Haines & DeBell 1979
Ceanothus spp.	60	"
Coriaria spp.	90 - 20	Fortin *et al* 1979
Elaeagnus spp.	2 - 15	Haines & DeBell 1979
Hyppophae spp.	80 - 197	"
Myrica spp.	9 - 15	"

*Compiled by Fortin and Carlisle (1982).

5.4.1. *Nitrogen fixation by free-living organisms*

Free-living bacteria capable of fixing nitrogen are either aerobic, anaerobic or facultative anaerobic. The aerobic N-fixers, Azotobacter and Beijerinckia are generally absent from acid forest soils (Chang and Knowles, 1965; Jurgensen and Davey, 1971). Azotobacter spp. have a low tolerance for acidic soils and are rarely found in soils having a pH lower than 6. In Quebec these organisms occur sporadically but are confined to soils having a pH greater than 6.5 (Brouzes et al., 1969). Beijerinckia, on the other hand, are more acid tolerant, having an optimum pH of 4-5. Although Beijerinckia spp. are prevalent in the tropics, small populations can be found in temperate soils and in the polar regions (Jurgensen and Davey, 1971).

Anaerobic nitrogen-fixing bacteria are invariably classified as Clostridium spp. These organisms found in tropical and temperate soils, are said to be resistant to acid conditions because they form endospores (Jurgensen and Davey, 1970). Anaerobic conditions generally favor nitrogen fixation activity. Rice et al. (1967) showed that maximum rates could be obtained where both aerobic and anaerobic sites were present. Jorgensen and Wells (1971) found that waterlogging did not initiate N fixation in inactive samples, but often enhanced rates in active samples. Added forest litter sometimes appeared to increase fixation rates in waterlogged forest soils studied by Brouzes et al. (1969), while these organic carbon additions generally reduced rates in aerobic incubations.

Jurgensen and Davey (1971) found Bacillus polymyxa to be the most common nitrogen-fixing species isolated from a number of forest soils. Chang and Knowles (1965) noted that nitrogen fixation during anaerobic incubation was significantly correlated with populations of "aerobic" bacteria and suggested that facultative anaerobes such as Bacillus spp. rather than Clostridium might be responsible. These Bacillus spp. have commonly been isolated from acidic soils.

Other bacteria belonging to the genera Enterobacter, Klebsiella, Pseudomonas, Achromobacter, Spirillum and Micrococcus can also fix nitrogen (Fortin et al., 1979).

Nitrogen fixation is also carried out by some blue green algae in association with plants. For example, Nostoc spp. have been found associated with certain bryophytes, liverworts such as Blasia spp. lavicularia spp., and with moss Hapalosiphon spp. Other such relationships exist between Anabaena, Nostoc and gymnosperms (Stewart, 1970, Burns and Hardy, 1975) and the ferns, Azollae (Peters et al., 1976).

Lichens represent a special kind of N-fixing symbiosis. They are composed of a fungus living in association with a blue-green alga (cyanobacterium). Among those which fix nitrogen are Collema granosum, Leptogium lichenoides, Peltigera practextata, P. polydactyla, P. pruinosa, Collema pulposum and Stereocaulon spp. The associated cyanobacterium is a member of Nostoc spp. Lichens Lichina pygmaea and L. confinis associated with Calothrix spp. can also fix nitrogen (Stewart, 1970).

Obtaining an accurate estimate of free-living nitrogen fixation requires attention to a number of potential sites of activity. Measurable nitrogen fixation has been reported in the canopy of Douglas-fir stands (Jones et al 1974) and in the rhizosphere of New Zealand conifers (Silvester and Bennett, 1972), although rates in both studies were less than 1 kg ha^{-1}yr^{-1}. Todd et al. (1978) made N-fixation measurements in a variety of specific microhabitats in a southern U.S. deciduous forest, including leaves, trunks, and roots of trees, surface litter, decomposing logs, organic soil horizons, and mineral soil. They found maximum activity in mineral soil and rotting logs, and total inputs of 12.5 kg ha^{-1} yr^{-1}. Jorgenson (1975) measured up to 10 kg N ha^{-1} yr^{-1} fixed in southern swamps but studies in northern deciduous forests (Tjepkema 1979; Roskoski 1980) indicate much lower rates, of 2 kg ha^{-1} yr^{-1} or less.

Evidence that N fixation may be significant in wood decay processes was cited earlier. Rotting logs often persist for long periods as recognizable organic substrates in forests and appear to contribute significantly to maintenance of organic matter levels in soil (McFee and Stone 1966). Therefore, low rates of fixation, accrued over an entire forest rotation, make a significant contribution to total net nitrogen inputs. Cornaby and Waide (1973) estimated that fixation in decaying chestnut logs accounted for 1.774 kg N $ha^{-1}yr^{-1}$ on a total watershed basis, and represented an annual input of about 4.1% of the total N found in the logs themselves. Larsen et al. (1978) indicated that brown-rotted logs, which tend to persist longer than logs decayed by white rot, have somewhat higher N fixation rates. They estimated that 0.735 kg N $ha^{-1}yr^{-1}$ was fixed in these logs. Roskoski (1980) measured similar rates in the northeastern U.S., and found that rotting logs were the only significant site of N fixation in the forest that she studied. One reason for the importance of woody litter is its ability to retain considerable amounts of water, and support anaerobic microsites, even during relatively dry periods (Larsen et al. 1978).

5.4.2. *Symbiotic nitrogen fixation*

In contrast to the low rates of N-fixation by free-living organisms are the high rates obtained in certain root nodule associations. Two groups of N-fixing of microorganisms form root nodules in a symbiotic relationship with higher plants. Rhizobia spp. are associated with many legumes. The legume-Rhizobium systems have significant commercial implications in agriculture. However, leguminous trees are more common in tropical forests than in temperate forests. Youngberg and Wollum II (1968) noted that of the thirty-three species (17 genera) which occur in North America, only six species (5 genera) would have commercial potential. Many are found in the arid and semi-arid areas of the southwest U.S. extending into Mexico. The high occurrence of legume-Rhizobium symbionts in the tropics is presumed to be an adaptation to high competition for available soil nitrogen in many tropical soils. In North America, the black locust, (Robinia pseudoacacia) is an important pioneer leguminous tree species in second growth stands in the Appalachians.

An actinomycete, designated as Frankia spp. (Becking, 1970) is the other N-fixing organism forming root nodules. These Frankia spp. are associated with non-leguminous plants. Nitrogen fixation by symbiosis other than legumes has been reviewed by Allen and Allen (1965); Bond (1963, 1967) and Youngberg and Wollum II (1968) among others. More than 100 species from 15 genera of nodulated non-leguminous plants are known. Many are distributed widely throughout North American forests and ranges. Table 2, taken from Burns and Hardy (1975) lists some of these. Some occur as regular components of climax vegetation while others occur as pioneer species after disturbance or deposition of fresh soil deposits such as volcanic ash, glacial till, or sand dunes (Youngberg and Wollum II, 1968).

Species of Ceanothus and Purshia are dominant understory plants in open ponderosa pine of the Northwest while Shepherdia can be found under similar stands of the Rockies. Many species of Alnus dominate stream banks. Many Ceanothus species are also good pioneer after disturbance. Species of Myrica, Dryas and Alnus are common pioneer plants on burns or other disturbances on sandy soils in northern coniferous forests. Red alder form nearly pure stands following logging or burning in the Pacific Northwest.

The biology and ecology of Frankia is not well understood. This is partly due to difficulties encountered in the past in the isolation of this organism in pure cultures. Baker and Torrey (1979) reported that some 40 attempts were made to isolate Frankia before Callahan et al. (1978) obtained a pure culture using an enzymatic method. Four other methods have produced Frankia in pure cultures; sucrose density gradient centri-

Table 2. **Nitrogen-fixing non-leguminous angiosperms.**

Order	Family	Genus	Known nodulated species/total species
Coriales	Coriariaceae	Coriaria	12 / 15
Myricales	Myricaceae	Myrica	11 / 35
		Comptonia	
Fagales	Betulaceae	Alnus	25 / 35
Casuarinales	Casuarinaceae	Casuarina	14 / 45
Rhamnales	Elaeagnaceae	Elaeagnus	9 / 45
		Hippophae	1 / 1
		Shepherdia	2 / 3
	Rhamnaceae	Ceanothus	30 / 55
		Discaria	1 / 10
Ericales	Ericaceae	Arctostaphylos	1 / 40
Rosales	Rosaceae	Dryas	1 / 4
		Purshia	2 / 2
		Cercocarpus	1 / 20

taken from Burns and Hardy, 1975.

fugation (Baker et al., 1979), a serial dilution (Lalonde, 1979) selective incubation (Quispel and Burggraaf, 1981) and osmium tetroxide (OsO_4) treatment (Lalonde et al., 1981). Lalonde and his coworkers have produced more than 200 isolates using the OsO_4 technique (personal communication). All isolates were found to be infective, forming nodules in 6-10 days after inoculation. Other successful inoculation trials were also reported (e.g., Houwers and Akkermans, 1981).

It appears that yield and nodule formation by Frankia are greatly enhanced in soils where organic matter levels are high, or has been supplemented with a substrate such as farmyard manure. Nitrogen fixation does not occur when Frankia is in the hyphal stage, and its onset coincides with production of vesicles within the roots (Mian and Bond, 1978). In the field, urea was found to repress nodulation while moderate levels of nitrate (15-30 ppm) were stimulatory (Zavitkovski and Newton 1968). Alder soils are characterized by active nitrification in spite of acid conditions, and it should be pointed out that wet conditions are most favorable for high nitrogen fixation activity (Wollum and Davey 1978).

Using nitrogen-fixing trees for improved forest productivity has enormous potential especially where logging practices have been designed so as to maintain soil organic matter and water-holding capacity. Present use of actinorhizal plants includes recolonization of disturbed land, in shelter belts, and forestry interplanting. Implications of using N-fixers to supply nitrogen have been discussed by others (McIntyre and Jeffries, 1932; Finn, 1953; Red'ko, 1958; Tarrant, 1961; Dale, 1962; DeBell and Radwan, 1979; Hansen and Dawson, 1982; Fortin and Carlisle, 1982). Estimates of nitrogen inputs in pure and mixed alder stands have been reported by many and summarized by Binkley (1981). In short, the use of nitrogen-fixing symbioses has benefits other than increased nitrogen inputs to forestry. Judicious exploitation of these systems can also improve soil organic matter levels, a desirable condition which positively influences other important properties such as ion exchange capacity, moisture stress, microbial activity and buffer capacity. The end result could be greater yield and site productivity.

6. MANAGEMENT IMPACTS

The forest soil microflora may be modified directly by introducing mycorrhizae or nitrogen-fixing actinomycetes, usually in conjunction with a suitable host tree species. Nearly any forest management practice will have an indirect impact. This review can do little more than point to some areas of current interest and suggest sources of additional information for the interested reader.

6.1. Harvesting

Timber harvest may lead to appreciable losses of soil nutrients, as occurred in the Hubbard Brook study (see the section on Nitrification). Nitrate, formed by autotrophic nitrifying bacteria, is a mobile anion. Losses of nitrate-N will be accompanied by cation losses.

Vitousek and Mellillo (1979) have reviewed current knowledge on the nitrogen cycle in disturbed forest ecosystems. They discuss several factors which may lead to increased mineral nitrogen pools after harvesting- higher soil temperature, excess moisture, and release of litter from mycorrhizal inhibition of decay as demonstrated by Gadgil and Gadgil (1978). However, other factors act to retain this mineral-N, including rapid vegetation regrowth (may include coppicing hardwoods), and microbial immobilization in the decaying slash. Timber cutting shifts the balance from immobilization to net mineralization, but the magnitude of "excess mineralization" may vary greatly from site to site. Even if excess amounts of NH_4^+–N are produced, nitrification need not follow. Nitrifier populations may be low, or be inhibited by shortage of another nutrient such as phosphorus. Prompt revegetation of the cut-over area is the most certain strategy for minimizing nitrogen losses.

Surprisingly little work has been reported on the effects of clear-cutting upon microbial populations and biomass, considering the importance of this harvesting technique in forest management. Two Scandinavian studies have been made in areas where regeneration has failed. Baath (1980) measured changes in total fungal biomass (agar-film technique) and fluorescein-diacetate "active" hyphae after a 120-year Scots pine stand was cut in Sweden. Logging slash was removed from some plots, and double amounts placed on others. Both total and "active" fungal hyphae declined rapidly, even where slash was present. In three years, total length of fungal biomass decreased from 15,000, 1,150 and 750 m g^{-1} to 9,000, 800 and 400 m g^{-1} in the F & H, A and B horizons, respectively. In a nearby 9-year old clear cut, values were 165, 12.5, and 2.5 m g^{-1} in the same three horizons. Several explanations were offered for these rapid declines. A thick layer of lichens and mosses immobilized rapidly leached nutrients and inhibited upward growth of fungi into the slash from underlying soil. Root litter production, which had been the major detrital input in the intact forest, was eliminated. Disappearance of mycorrhizal fungi was responsible for a large part of the fungal biomass decrease. Production of fruiting bodies ceased. A rapid drying of the F and H layers was observed, but could not account for hyphal reductions in the underlying mineral soil.

In contrast, bacterial numbers in spruce forest soil were observed to increase from $1.32 \times 10^6\ g^{-1}$ in an uncut stand to a maximum of $3.99 \times 10^6\ g^{-1}$ in a stand cut seven years previously (Sundman et al. 1978). A 13-year-old clear cut showed reduced numbers, at $1.72 \times 10^6\ g^{-1}$. Parallel trends were seen in the rate of weight loss of cellulose strips incubated in the field in litter bags, and in soil respiration measured with an infra-red gas analyzer in the lab. CO_2 evolution in the 13-year-old clear cut was less than the control. Differences were shown to be significant using analysis of variance on the log-transformed data.

Initial increased activity was thought to reflect decay of dead roots and felling residues. This was followed by decreases to normal or subnormal levels, "reflecting the impoverishment due to lack of the original plant cover." Bacterial isolates, characterized on the basis of 36 physiological tests, showed significant changes in the 7-year-old clear cut, especially in the mineral soils (Niemela and Sundman 1977). Numbers of lipolytic and caseolytic organisms increased, and acid tolerance declined, though some reversion toward control populations occurred at 13 years after cutting. It appeared that cessation of root activity had a greater impact on the microflora than the disappearance of leaf litterfall. It was concluded that "if bacterial populations found in normal coniferous forest soils contribute to successful establishment of seedlings...at least 10, possibly many more, years of recovery after clear-cutting might, under severe conditions, be necessary for successful reforestation."

The effect of forest clearing seems to be a reversion to conditions similar to agricultural soils. Bacterial decay tends to replace fungal activity. Decomposition shifts from organic horizons to mineral soil, as nutrients and soluble carbon compounds leach downward. Surface conditions become less favorable for microbial activity due to excessive moisture and temperature fluctuations. Fine roots also become relatively more numerous in the mineral soil (Grier et al. 1981), reflecting these altered decomposition patterns.

6.2 Fire

Fire is widely used to facilitate site access after logging, to enhance the regeneration of selected tree species, and to eliminate competing understory species. Fire is also a dominant influence in many natural forests, where it may replace microbial decay as the primary agent of mineralization (St. John and Rundel 1976). Severe fires are highly destructive, while a fire which is confined to the upper soil organic horizons may have a positive effect on nutrient turnover and tree growth.

Although microbial populations decrease immediately following fire, recovery occurs within a few days, after which numbers are higher in burned areas. Ahlgren and Ahlgren (1965) found that increased bacterial counts in a burned jack pine stand were closely correlated with measured increases in inorganic soil nutrients (N, P, K, Ca, Mg). Fungal population increases were slower and of lesser magnitude. A post-fire shift in the species composition of soil fungi, from common litter inhabitants (Penicillum, Trichoderma, Chrysospovium) to saprophytes and weak parasites (Phoma, Botrytis), was noted in a subalpine spruce forest (Bissett and Parkinson 1980). The saprophytic fungi appeared concurrently with the herbs and grasses colonizing the burned area. Bissett and Parkinson (1980) also showed that cellulose breakdown was enhanced on the burnt site, in part due to higher soil temperatures. After six years, many fungi which had been eliminated from the burned organic horizons reappeared. In Quebec, Penicillum citrinum, Trichoderma hamatum, and T. polysporum were relatively more abundant in spruce stands aged 104 and 137 years post-fire than a stand 2 years post-fire. The removal and subsequent buildup of organic matter is the major factor causing these changes (Lucarotti et al. 1978).

Most of these studies only report changes in microbial populations on a dry weight basis. Jorgensen and Hodges (1970) compared a southern pine forest which received annual prescribed burning with an unburnt control, and with a forest which had been burned 8 years previously. Annual burning greatly reduced bacterial populations (control-21.53×10^6 cm^{-2}, annual burn- 3.68×10^6 cm^{-2}) in the combined F+H horizon. Numbers were elevated, at 25.19×10^6 cm^{-2}, in the 8-year post-fire site. Fungal populations showed similar trends-0.64×10^6 cm^{-2}, 1.16×10^6 cm^{-2}, and 0.16×10^6 cm^{-2} in the control, 8-yr and 1-yr sites, respectively. However, the authors found "no evidence that soil metabolism was impaired" by the reduction in litter amounts and microbial numbers on the annually burned site.

Pathogenic fungi may increase following fire. Cylindrocarpon destructans shows a position response to extracts from burnt litter, whereas Penicillium and Trichoderma are inhibited (Widden and Parkinson 1975). Rhizina undulata, a root rotting fungus, commonly appears on sites where logging slash has been burned (Ginns 1968, Morgan and Driver 1972). Fire scars on living aspen trees are a major infection site for the heart rotting fungus Fomes ignarius (Schmitz and Jackson 1927). On the other hand, excessive amounts of unburnt logging residues may create moist and shady conditions, so that sporophores of potential pathogens "appear in excessive numbers on the debris of a sale area" (Weir 1923).

Other effects of fire, including its impacts on mycorrhizae and nitrogen transformations, are reviewed by Harvey et al. (1976). These authors remark that "the limits and conditions under which the rejuvenative and protective silvicultural benefits provided by fire exceed its potential damage" are not yet defined.

6.3. Fertilization

It has often been proposed that nitrogen additions can overcome nitrogen deficiencies on poor soils. Both forest fertilization experiments and laboratory incubations have been used to test this proposal. Roberge and Knowles (1966, 1967) found that addition of 400 lb./acre urea-N to a black spruce stand resulted in rapid ammonification to NH_4^+-N in 3 days, accompanied by a litter pH increase of 1.5 units. Fungal populations increased 4-fold; bacterial populations increased 3-fold. If samples returned to the lab were treated with another dose of urea, bacteria, but not fungi, showed a further increase to a maximum in 3 days. Populations then remained quite stable during a prolonged incubation. These changes were not reflected in changes in ureolytic populations. Presumably the effect was rapid mortality of existing populations, followed by establishment of a new community of organisms adapted to a higher pH/N regime.

A study of urea fertilization in connection with thinning (Roberge et al. 1970) indicated that the slash produced in thinning immobilized some added N, but most N was still in the "exchangeable" NH_4^+ pool even after 5 years. It was suggested that low pH, inhibitors, and low availability of humus constituents limit the incorporation of nitrogen in slash and its subsequent breakdown. It might be added that relatively high populations of fungi (especially in the L horizon) and bacteria (F_1 and F_2 horizons) persist in fertilized plots after 5 years, compared with the control. These increased microbial populations will compete with trees for the added fertilizer nitrogen.

Urea has two effects on forest humus: increase in nitrogen, and increase in pH. The liming effect extracts soluble carbon compounds from humus, allowing bacteria to multiply (MacDonald 1979). More urea-N is immobilized than NH_4^+–N in tracer experiments with ^{15}N compounds added to raw humus, while NO_3^-–N is relatively inert (Overrein 1967).

In one forest fertilization experiment, lime alone increased CO_2 evolution while immobilizing nitrogen; conversely, NH_4^+ alone decreased respiration while increasing mineral N production, at least for a 6-month period (Williams 1972). Phosphate addition overcame the depressive effect of nitrogen upon respiration; thus, "the microbial activity was limited in N-treated plots by a reduction of available P resulting from residual N fertilizer." Phosphorus alone had little effect in this study, but has been shown elsewhere to promote immobilization of N and reduced respiration (Nommik 1978). Other field experiments (Adams and Cornforth 1973) and lab experiments (Salonius 1972; Foster et al. 1980; Moore 1981) have been carried out, with varying results.

How should these findings be interpreted? It is hard to maintain that nitrogen limits humus decomposition (Roberge et al. 1970) when additions of

NH$_4^+$ depress microbial respiration. Liming experiments suggest that available organic carbon is limiting, since microbial populations increase greatly after urea additions. This theory is advanced by Salonius (1972) and Foster et al. (1980). In reality, it is likely that both available energy and any of a number of nutrient elements will be limiting in nutrient-poor forest soils. Addition of one element in excess is likely to induce deficiencies of other elements. Enhanced humus decomposition will not lead to improved tree growth if nutrients remain immobilized in microbial biomass.

The assumption that buildup of forest floor material is undesirable per se (Mahendrappa 1978; Foster et al. 1980) can be challenged on two grounds. First, the forest floor in a productive stand represents an accumulation of available nutrients. The high cation exchange capacity of its humic substances ensures the retention of additional nutrient inputs in rainfall. Organic matter accumulation and decomposition will approach a steady state, in which overall nutrient turnover can be quite rapid despite the existence of a pool of fresh "immobilizing" litter. Second, competition for nutrients is largely between heterotrophic fungi and mycorrhizal roots. Litter decay inhibition by the mycorrhizal roots may confer a selective advantage upon the mycorrhizal/host tree symbiosis in obtaining these scarce nutrients, making them available when tree growth requirements are at a maximum (e.g. early spring). A practical approach to forest fertilization experiments might focus upon growth responses of various tree species rather than reduction of litter via enhanced microbial degradation.

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